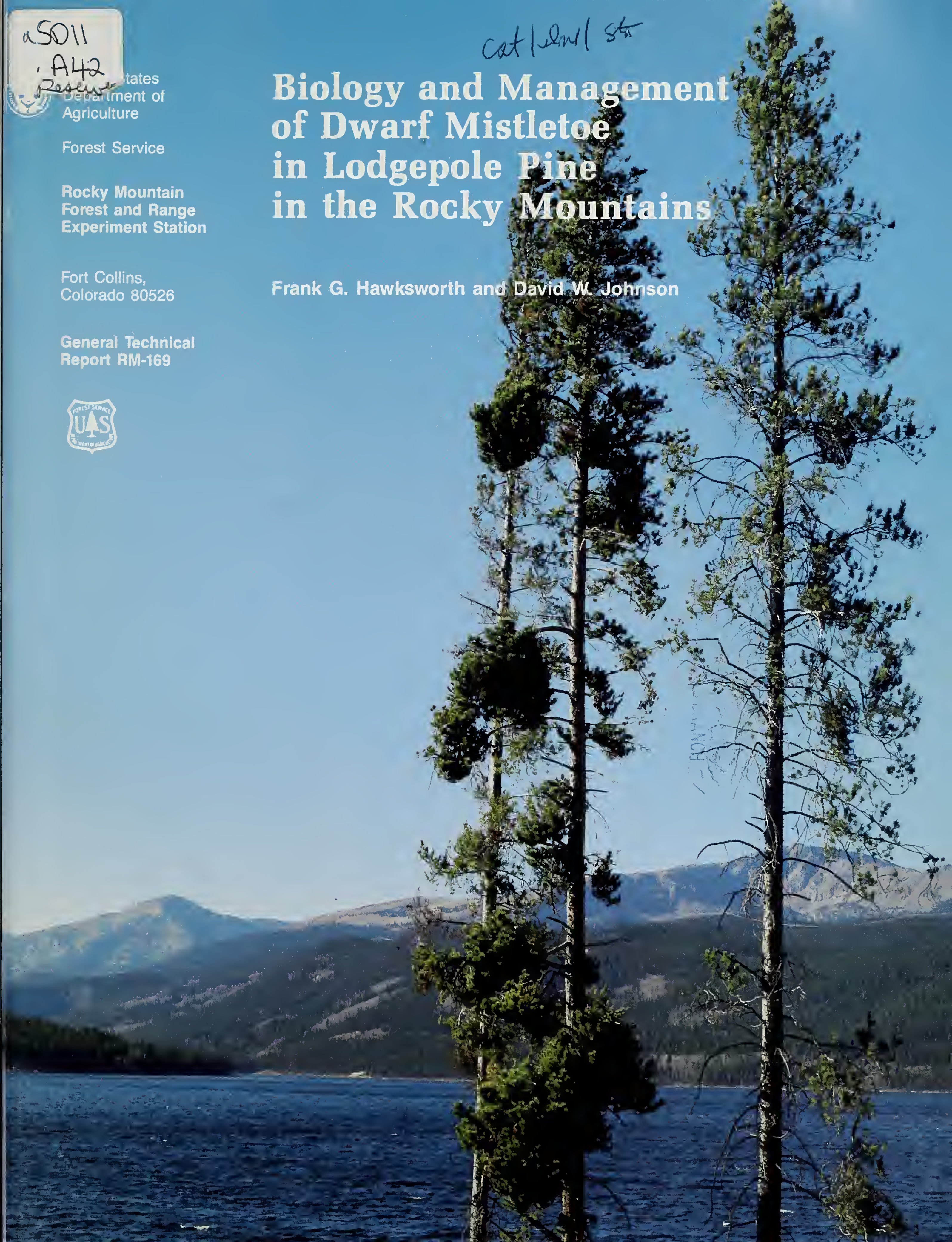

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United States
Department of
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Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-169

Biology and Management of Dwarf Mistletoe in Lodgepole Pine in the Rocky Mountains

Frank G. Hawksworth and David W. Johnson

Dedication

Oscar J. Dooling, 1931–1987

This work is dedicated to the memory of Oscar J. Dooling, long-time Forest Pathologist with the Forest Pest Management Unit, USDA Forest Service Regional office in Missoula, Montana. Oscar's strong interest and helpfulness in providing on-the-ground forest disease assistance for foresters throughout the Rocky Mountains was well known. He recognized the need for and encouraged us to write this compilation on lodgepole pine dwarf mistletoe as an aid to forest managers for controlling this widespread pest.

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Biology and Management of Dwarf Mistletoe in Lodgepole Pine in the Rocky Mountains

Frank G. Hawksworth
Rocky Mountain Forest and Range Experiment Station[1]

David W. Johnson
Timber, Forest Pest, and Cooperative Forestry Management
Rocky Mountain Region

Abstract

This publication synthesizes the vast literature on lodgepole pine dwarf mistletoe (*Arceuthobium americanum*) and adds some new information on biology of the parasite. Although dwarf mistletoe has been recognized as a serious parasite of lodgepole pine for more than 75 years, its routine operational control through forest management has been primarily a development over the past two decades. This report discusses silvicultural control of dwarf mistletoe in various types of stands where fiber production is the primary goal, and also in forests used mainly for recreation.

[1] *Headquarters is in Fort Collins, in cooperation with Colorado State University.*

Contents

Biology and Management of Dwarf Mistletoe in Lodgepole Pine in the Rocky Mountains

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INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl.) is the most widely distributed conifer in western North America. It ranges from the central Yukon to Baja California, and east to Alberta and South Dakota (Critchfield and Little 1966). The commercial area of lodgepole pine is nearly 63 million acres (25.5 million ha), with more than 50% of it in British Columbia (McDougal 1975, Wellner 1975). The lodgepole pine growing stock is about 82 billion ft^3 (2.32 billion m^3), and its annual harvest is about 530 million ft^3 (15 million m^3). About one-third of the growing stock and one-fourth of the annual lodgepole pine harvest are in the United States, with most of it in the Rocky Mountain states of Montana, Idaho, Wyoming, and Colorado.

An excellent synthesis of information on lodgepole pine and its management appears in the proceedings of a recent symposium (Baumgartner et al. 1985). Other recent references that contain much useful information on lodgepole pine are a bibliography of the literature on the species (Grewal 1987) and symposia proceedings on subalpine forests of the Rocky Mountains (Troendle et al. 1987) and future forests of the Mountain West (Schmidt 1988).

Lodgepole pine has four geographic subspecies (Wheeler and Critchfield 1985):

- *P. contorta* ssp. *contorta* (shore pine)
- *P. contorta* ssp. *murrayana* (Balf.) Critchfield (Sierra-Cascade lodgepole pine)
- *P. contorta* ssp. *bolander* (Parl.) Critchfield (Mendocino White Plains shore pine)
- *P. contorta* ssp. *latifolia* (Engelm. ex Wats.) Critchfield (Rocky Mountain lodgepole pine).

The last is the most widespread subspecies and is the type referred to throughout the rest of this paper.

Lodgepole pine is plagued by many pests, the two most important of which are dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) and mountain pine beetle (*Dendroctonus ponderosae* Hopk.). The former is the subject of this paper; the latter has been the subject of recent reviews (e.g., McGregor and Cole 1985).

Dwarf mistletoe is the most widespread and damaging disease agent in lodgepole pine throughout its range, and has been recognized as a serious pest for more than 70 years (Mason 1915). Because of the importance and wide distribution of *Arceuthobium americanum*, both in the United States and Canada, more literature has been written on it than for any other dwarf mistletoe. This report synthesizes information from the most significant of the more than 1,100 publications on the species that relate to its biology, ecology, damage, and silvicultural control, and also includes some new information.

HOSTS, DISTRIBUTION, AND ABUNDANCE

Hosts

Lodgepole pine is the primary host of *A. americanum* (table 1). Although no susceptibility tests have been made, observations suggest that the Pacific Coast subspecies (*P. contorta* ssp. *murrayana*) and the Interior subspecies (*P. contorta* ssp. *latifolia*) are about equally susceptible. Shore pine (ssp. *contorta*) also is susceptible, but there are only a few areas in north-coastal British Columbia where this tree occurs within the range of *A. americanum* (Smith and Wass 1979).

Arceuthobium americanum also parasitizes jack pine (*Pinus banksiana* Lamb.) from northern Alberta to extreme western Ontario. The dwarf mistletoe also attacks the lodgepole pine-jack pine hybrid in northern Alberta (Hawksworth and Wiens 1972). Some secondary, occasional, rare hosts and immune tree species appear in table 1.

Distribution

Arceuthobium americanum is one of the most widely distributed dwarf mistletoes in North America, ranging

Table 1.—Natural hosts of *Arceuthobium americanum* in western North America (adapted from Hawksworth 1975).

Principal	*Pinus contorta* ssp. *latifolia* *Pinus contorta* ssp. *murrayana* *Pinus contorta* ssp. *contorta*[1]
Secondary	*Pinus ponderosa* var. *scopulorum*
Occasional	*Pinus albicaulis* *Pinus flexilis* *Pinus ponderosa* var. *ponderosa*
Rare	*Picea glauca* *Picea engelmannii* *Picea pungens* *Pinus aristata* *Pinus attenuata*[2] *Pseudotsuga menziesii*[3]
Immune	*Abies concolor* *Abies grandis* *Abies lasiocarpa* var. *lasiocarpa* *Abies magnifica* *Larix occidentalis* *Tsuga mertensiana*

[1]*Known only from a few areas in coastal British Columbia on this host.*

[2]*Unconfirmed reports in southwestern Oregon.*

[3]*Extremely rare on this host; known from only one locality in northern Utah (Hawksworth and Wiens 1972), one in Alberta (Muir 1973), and one in Colorado (R. L. Mathiasen collection in USDA Forest Service Forest Pathology Herbarium in Fort Collins, CO).*

from northern Alberta (nearly 60° N lat.) to central Colorado (38° N lat.) and central California (35° N lat.) on lodgepole pine, and on jack pine from Alberta to western Ontario (Hawksworth and Wiens 1972) (fig. 1). Dwarf mistletoe occurs essentially throughout the range of *Pinus contorta*, with the notable exception of stands west of the Pacific Crest in Oregon and Washington.

Abundance

Recent surveys indicate the magnitude of the lodgepole pine dwarf mistletoe problem in the Rocky Mountains (table 2). Surveys in the Intermountain Region (southern Idaho, western Wyoming, and Utah) show that about 60% of the lodgepole pine stands are affected. For the Rocky Mountain Region (Colorado and Wyoming east of the Continental Divide), the comparable figure is 51%. Infection in lodgepole pine stands in Montana National Forests ranges from 18% to 52% and averages 35%.

BIOLOGY

The Mistletoe Plant

Shoots

Arceuthobium americanum plants are dioecious and typically 5 to 8 cm tall (Hawksworth and Wiens 1972)

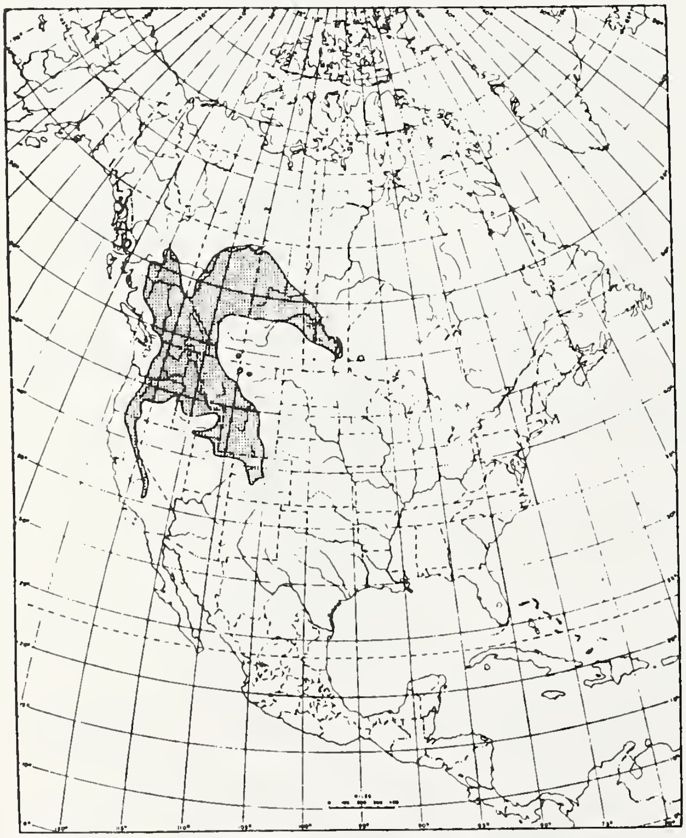


Figure 1.—General distribution of lodgepole pine dwarf mistletoe in North America.

Table 2.—Incidence of lodgepole pine dwarf mistletoe by National Forests in the Rocky Mountains.

Region, State, National Forest	Incidence of *A. americanum* in lodgepole pine type stands (% affected)
Northern Rocky Mountain Region	
MONTANA[1]	
Beaverhead N.F.	52
Bitterroot N.F.	44
Custer N.F.	28
Deerlodge N.F.	47
Flathead N.F.	18
Gallatin N.F.	42
Helena N.F.	35
Kootenai N.F.	22
Lewis and Clark N.F.	37
Lolo N.F.	23
Subtotal	35
IDAHO[2]	
Nez Perce N.F.	27
Idaho Panhandle N.F.	27
Clearwater N.F.	8
Subtotal	21
Intermountain Region[3]	
CALIFORNIA	
Toiyabe N.F.	17
IDAHO	
Boise N.F.	57
Caribou N.F.	68
Challis N.F.	70
Payette N.F.	50
Salmon N.F.	59
Sawtooth N.F.	71
Targhee N.F.	79
UTAH	
Ashley N.F.	58
Uinta N.F.	28
Wasatch N.F.	34
WYOMING	
Bridger-Teton N.F.	67
Subtotal	60
Rocky Mountain Region[4]	
COLORADO	
Arapaho-Roosevelt N.F.	48
Grand Mesa-Uncompaghre-Gunnison N.F.	52
Pike-San Isabel N.F.	43
Routt N.F.	52
White River N.F.	36
WYOMING	
Bighorn N.F.	36
Medicine Bow N.F.	60
Shoshone N.F.	64
Subtotal	51

[1]*Data from Dooling and Eder (1981).*
[2]*Estimates provided by O. J. Dooling (personal communication, 1985).*
[3]*Data from Hoffman and Hobbs (1985).*
[4]*Data from Johnson et al. (1981).*

(Plate I). The shoots are leafless, with whorled branching. Male and female plants usually occur in a ratio of 1:1. Female shoots tend to be greenish, while male shoots are typically more yellow, especially in the spring.

Male Flowers

The male flower has three or four segments, each with a single sessile anther (Plate I). The pollen grains are globose, spinulose, and about 20–25 microns in diameter. A nectary is found at the center of each flower. *A. americanum* flowers in the spring; flowering begins in late March and lasts until late June, but with a peak usually between early May and mid-June (Hawksworth 1965) (fig. 2).

Female Flowers and Fruits

The female flowers of *Arceuthobium* are small and inconspicuous. The perianth segment is two-parted (Plate I). The flowers are pollinated in the spring, and the fruits take 15–17 months to develop before they mature in late summer of the second season. The pollinated fruits attain about one-third of their final size during the first summer. As the fruits mature, the pedicel becomes elongated so that the original tip of the fruit is oriented downward (Plate I). At maturity, the single seed is forcibly ejected from the fruit at initial velocities up to 60 miles/hr (2,600 cm/sec) (Hinds and Hawksworth 1965). Seeds are dispersed for distances up to 50 feet (15 m), but typically for 15 feet (5 m) or less.

The period of seed dispersal lasts about 8 weeks, but is usually only 3–4 weeks at a given locality and year.

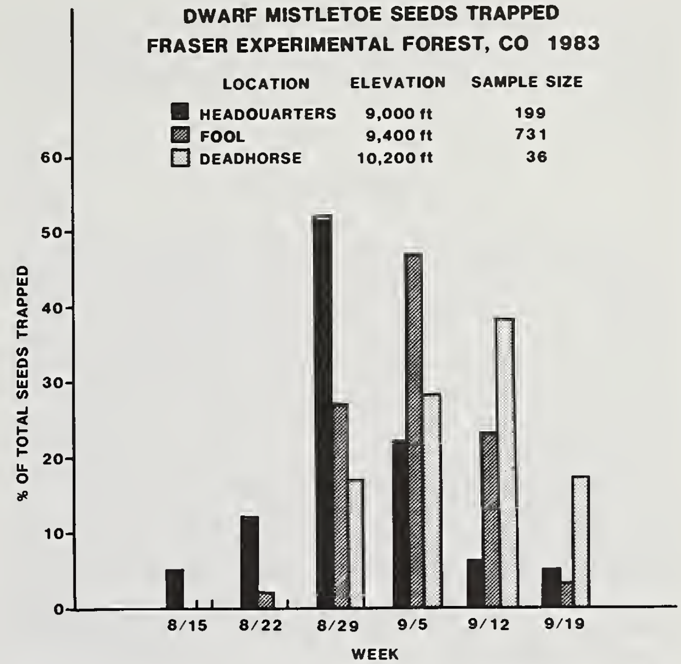


Figure 3.—Phenology of seed dispersal of lodgepole pine dwarf mistletoe at three elevations in the Fraser Experimental Forest, Colorado (Nicholls et al. 1984).

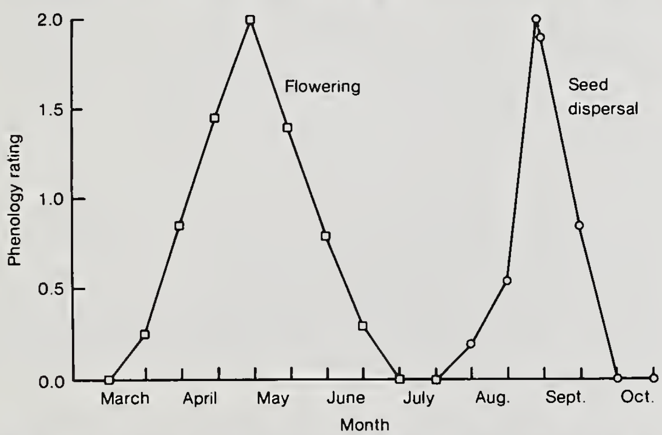


Figure 2.—Phenology of flowering and seed dispersal of *Arceuthobium americanum*. Based on about 240 populations from throughout the range of lodgepole pine. For phenological studies, we use a 5-point phenology rating system to classify individual populations:

0 - Flowering (or seed dispersal) not yet begun;
1 - " " " " begun but not at peak;
2 - " " " " near peak;
3 - " " " " past peak;
4 - " " " " over.

The results are then summarized by 2-week periods. Then a cumulative graph (0–4) is plotted; for this figure, the portion beyond 2.0 was inverted to show the peak, thus 3.0 (past peak) is here plotted as 1.0 and 4.0 (flowering and seed dispersal over) plotted as 0.0.

Seed dispersal begins in late July and lasts until early October, but with peaks usually between late August and late September (fig. 2). At a given locality, seed dispersal begins first at lower elevations. For example, on the Fraser Experimental Forest in Colorado, peak dispersal was about 1 week later for each 500-foot (150-m) increase in elevation (fig. 3) (Nicholls et al. 1984).

Pollination

Although dwarf mistletoes have the flower and pollen characteristics of insect-pollinated plants (limited pollen production, spinulose pollen, pollen dispersed in clusters, nectar, and odor production) (Hawksworth and Wiens 1972), their pollen is also disseminated by wind (Gilbert and Punter 1984, Player 1984). Penfield et al. (1976) concluded from a study of *A. americanum* and two other dwarf mistletoes in northern Colorado that these species are primarily insect-pollinated. About 20 species of pollen-bearing insects were found on *A. americanum*, the most important of which were an ant (*Formica fusca* L.) and a fly (*Philygra debilis* Loew.). Gilbert and Punter (1984) concluded that both insects and wind are involved in pollination of *A. americanum* on jack pine in Manitoba. Wind-borne pollen was found up to 1,300 feet (400 m) from the closest pollen source. Coppola (1988) found *A. americanum* pollen up to 1,680 feet (512 m) from the closest male plants in the Roosevelt National Forest in northern Colorado.

Life Cycle

A generalized life cycle of *A. americanum* appears in figure 4. The time from seed dispersal to infection, establishment of new plants, and flowering averages

about 6 years. The time from seed dispersal to production of the first shoots ranges from 2 to 8 years, with about two-thirds appearing in the third and fourth years (fig. 5).

Host Reactions

Dwarf mistletoes typically develop fusiform swellings on the host at the site of the infection (Plate II). These swellings are caused by increased growth in both host cortex and xylem. If infection occurs on relatively young host tissues, dormant host buds are stimulated, and dense masses of branches called witches' brooms subsequently develop (Plate III). Lodgepole pine dwarf mistletoe typically forms a unique type of witches' broom; these are systemic in that the root system of the parasite is incorporated into the apical meristem of the bud of the host twig (Hawksworth and Wiens 1972, Kuijt 1960). All branches on the broom are thus parasitized by the mistletoe. On these systemic brooms, clusters of the mistletoe shoots are formed at the interwhorl between annual growth segments.

Seed Dispersal

Few studies have been conducted on the distance of seed dispersal of *A. americanum*. Muir (1977) measured dispersal from two 10-foot (3-m) tall lodgepole pines in Alberta, where the number of seeds dispersed decreased logarithmically with increasing distance from the source trees. The maximum distance of seed flight from the crown circumference was 13 feet (4 m) from one tree, and 18 feet (5.5 m) from the other.

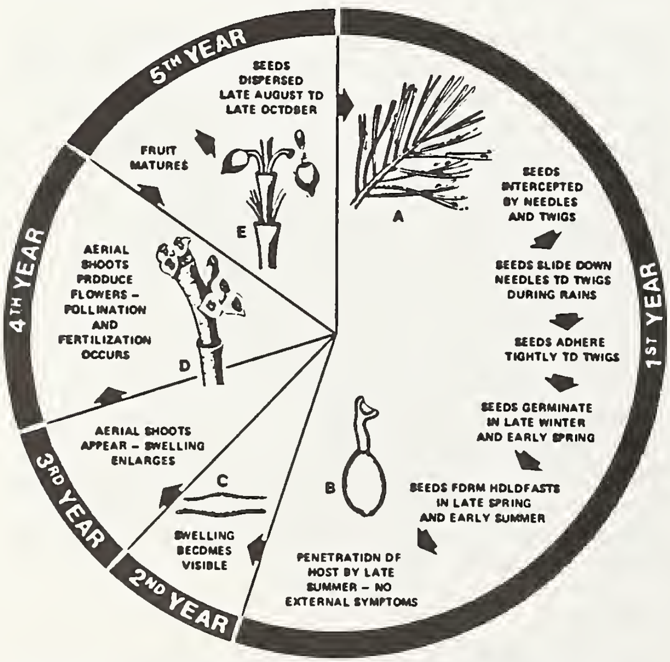


Figure 4.—Generalized life cycle of *Arceuthobium americanum* on lodgepole pine. Adapted, with permission, from Baranyay and Smith (1972).

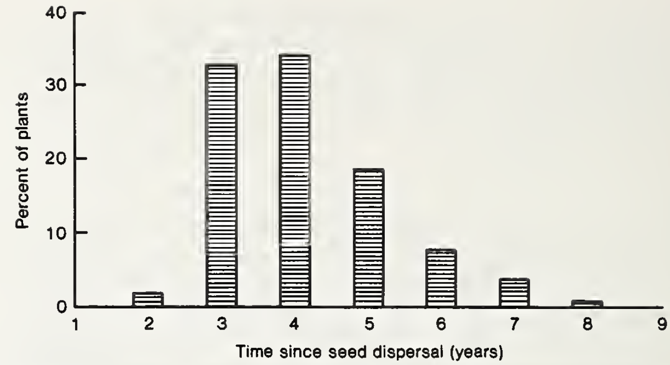


Figure 5.—Length of the incubation period from time of seed dispersal to appearance of first shoots. Basis: 469 plants on the Roosevelt National Forest, Colorado.

Distances of spread of *A. americanum* from larger trees is greater than for small trees. Average distances of seed dispersal from overstory trees to adjacent reproduction ranged from 22 to 28 feet (6.7–8.5 m) (Hawksworth 1958b, Hawksworth and Graham 1963, Muir 1970). Mean distance of spread from stands in Alberta was 28 feet (8.5 m) and up to 45 feet (13.7 m) from isolated residual trees (Muir 1970). Perhaps wind is more significant in dispersal from isolated trees than along stand edges.

Spread and Intensification

Local Spread

The rates of spread of *A. americanum* are fastest from overstory trees to adjacent reproduction. Spread through even-aged stands is considerably slower. Hawksworth (1958b) studied rates of spread in Colorado and Wyoming (fig. 6). In 20-year-old stands adjacent to an infested overstory stand, dwarf mistletoe progressed less than 30 feet (9 m) into the reproduction. In 30-year-old reproduction, the parasite spread 30 to 45 feet (9–14 m), depending primarily on the density of the young stand. Spread through young lodgepole pine is 1.5 times greater in stands in which the canopy has not closed than in stands with closed canopies. In 20-year-old stands, about 10% of the trees within 30 feet (9 m) of an infested mature stand were infected. In 30-year-old stands, infection in this zone approached 35%.

Beyond 30 feet from the residual stands, average rate of spread through even-aged open stands was 1.7 feet (0.5 m) per year, and 1.2 feet (0.4 m) per year in dense stands. Hawksworth and Graham (1963) conducted a more detailed study of overstory-understory spread in lodgepole pine in Colorado, Wyoming, and Montana. The average proportion of trees visibly infected in reproduction 10, 15, 20, and 25 years old was 3%, 9%, 18%, and 32%, respectively (fig. 7). Thus, the proportion of trees visibly infected essentially doubled each 5 years between ages 10 and 25. The amount of dwarf mistletoe was highest in reproduction on the better sites. Dissections of the oldest infections on the plots showed that 84% were infected before they were 11 years old. None

of the factors measured that were associated with the residual stand (e.g., stand mistletoe rating, tree height, etc.) or with the location of the study areas were correlated with amounts of infection in the reproduction. Spread from bole infections is generally minor (Walters 1974).

The proportion of the total number of young infected trees within various distances of the mature stand is shown in figure 8. Sixty-four percent of the infected trees were within 20 feet (6 m) of the residual stand, 89% within 30 feet (9 m), and 98% within 40 feet (12 m).

Long-Distance Spread

Very little is known about long-distance dispersal of *A. americanum* seed. The frequent occurrence of isolated pockets of infection beyond the limits of spread that could be accounted for by the explosive fruits alone confirms that there is some long-distance spread. The only study to quantify long-distance spread in *A. americanum* is by Hawksworth et al. (1987) on the Fraser Experimental Forest in Colorado. They surveyed for isolated, satellite infection centers in an otherwise mistletoe-free 70-year-old stand surrounded by heavily infested stands. They found 21 satellite centers in a 37-acre stand, or 0.6 per acre (1.4 per ha). The centers ranged from 39 to 213 feet (12 to 65 m) from the closest potential infection source. Ages of infection in the centers ranged from 4 to 50 years, but most were 10 to 20 years old. More than two-thirds of the satellite centers were near openings in the stands, probably because such areas are a more attractive habitat for birds, which are presumed to be responsible for long-distance dispersal of mistletoe seeds.

Hawksworth et al. (1987) and Nicholls et al. (1984) studied the potential animal vectors of lodgepole pine dwarf mistletoe on the same area on the Fraser Experimental Forest. They found dwarf mistletoe seeds being carried externally by 10 species of birds and four mammals (Plate IV). About 7% of the birds and mammals trapped carried mistletoe seeds, but this was as high as 22% during the 2-week period of peak seed dispersal.

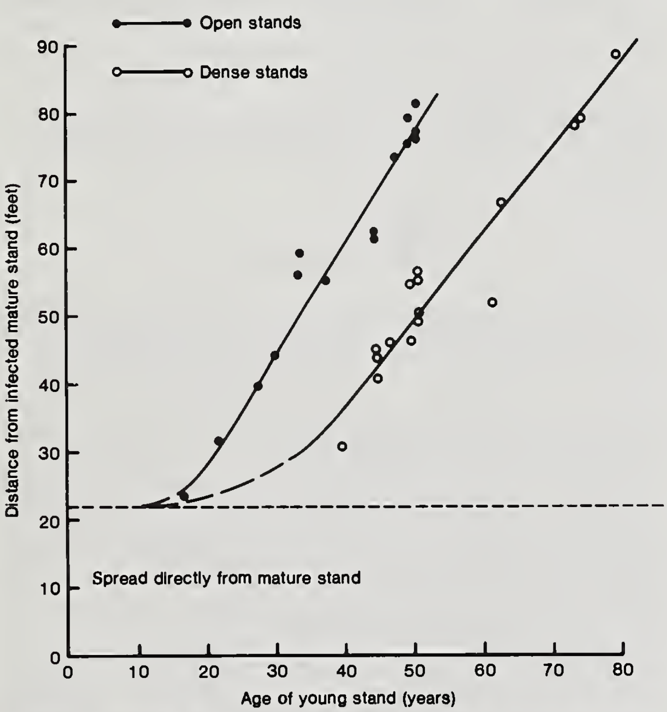


Figure 6.—Lateral spread of dwarf mistletoe from mature lodgepole pine stands into regeneration; based on 31 study areas in Colorado and Wyoming (Hawksworth 1958a).

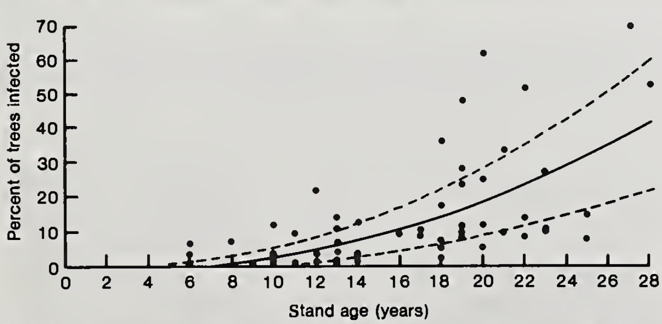


Figure 7.—Percent of young lodgepole pines infected within 30 feet (9 m) of infested residual stands on 79 plots in Colorado, Wyoming, and Montana. The dotted lines indicate 95% confidence intervals (Hawksworth and Graham 1963).

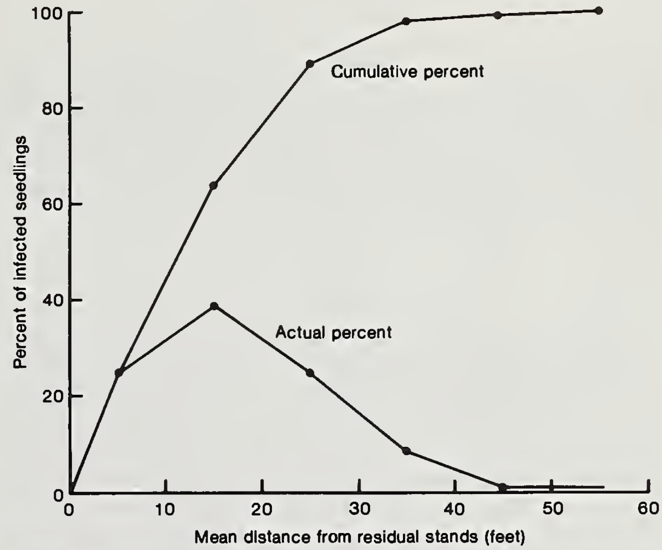


Figure 8.—Distance of infection in young lodgepole pine stands in relation to residual stands. Based on 325 infected trees in stands in Colorado, Wyoming, and Montana (Hawksworth and Graham 1963).

Intensification

Muir (1972) studied rates of intensification of *A. americanum* in young lodgepole pines in Alberta. In lodgepole pine from 15 to 26 years old, the number of dwarf mistletoe plants increased exponentially. During this 9-year period, the number of infections increased about four times every 5 years.

Hawksworth and Hinds (1964) studied even-aged lodgepole pine in Colorado and found that the average stand dwarf mistletoe rating (DMR) increased an average of about one DMR class in 14 years in stands 15 to 60 years old (fig. 9). The rate was somewhat slower in stands under 15 and those over 60 years old.

Biotic Associates

There are many biological associates of lodgepole pine dwarf mistletoe (Plate IV). Several fungi parasitize the shoots, fruits, and endophytic system; insects, mammals, and birds feed on the shoots; and the witches' brooms provide cover and nest sites for birds and squirrels (Hawksworth 1975).

Fungi

Cylindrocarpon (*Septogloeum*) *gillii* (Ellis) Muir is an occasional parasite of *A. americanum* in the United States and Canada (Hawksworth et al. 1977). *Wallrothiella arceuthobii* (Peck) Sacc. parasitizes mistletoe fruits and prevents seed formation. Although both fungi have some local influence on mistletoe populations, their overall effect is minor. Two other disease syndromes involving pine tissue and lodgepole pine dwarf mistletoe have been studied, but their potential as significant biological control agents has not been demonstrated: the "resin disease," caused by a complex of weakly parasitic fungal pathogens (Mark et al. 1976) and the blister rust fungus *Peridermium bethelii* (Hawksworth et al. 1983).

Insects

At least 10 species of insects feed on lodgepole pine dwarf mistletoe (Stevens and Hawksworth 1970, 1984). The most damaging are lepidoptera larvae; others that attack dwarf mistletoe shoots are plant bugs of the genus *Neoborella*. Neither the extent of the damage they cause nor their biological control potential have been determined. In some instances, birds forage for insects in clumps of dwarf mistletoe shoots and, thus, when fruits are ripe, may pick up and transport mistletoe seeds (see next section).

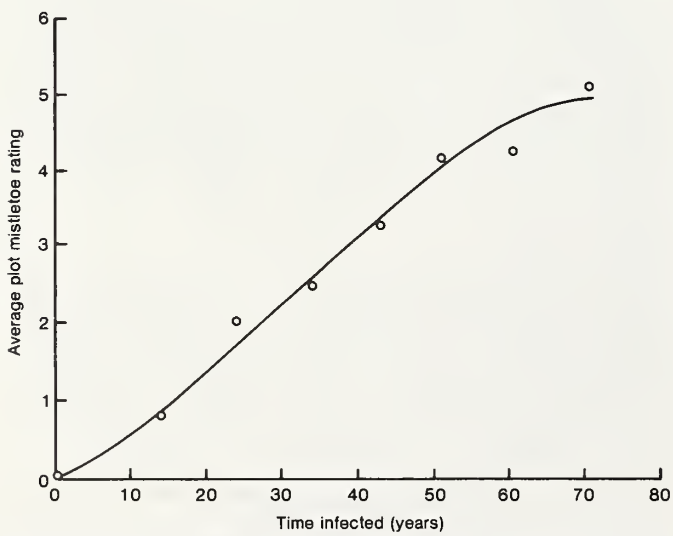


Figure 9.—Relationship between the time infected and stand dwarf mistletoe rating in lodgepole pine in Colorado. Based on 126 plots in stands 50 to 150 years old (from Hawksworth and Hinds 1964).

Birds and Mammals

Some birds (ruffed grouse, blue grouse, black-capped chickadee) are reported to eat dwarf mistletoe seeds (Hawksworth 1975), and red squirrels (*Tamiascuirus hudsonicus*) preferentially eat mistletoe-infected rather than healthy bark (Baranyay 1968). Craighead et al. (1973) note an unusual instance where dwarf mistletoe plants, which are rich in protein, are a major winter food for elk in the thermal areas of Yellowstone National Park, Wyoming.

ECOLOGY

Because of the intimate association of dwarf mistletoe with its lodgepole pine host, the ecological factors that affect the host also directly influence the parasite. Little information is available on the ecological interrelationships of dwarf mistletoes, but the limited research indicates that ecological factors are very important in mistletoe distribution and abundance. Some factors that have been studied are (1) plant associations or habitat types, (2) topography, (3) site factors, and (4) stand fire history.

Plant Associations

The first report of the association of vegetative types with a dwarf mistletoe was Dowding's (1929) study of *A. americanum* on *Pinus banksiana* in central Alberta. She showed that the parasite was much more common in the drier pine-moss association (71% of trees infected) than in the moister pine-heath association (5% of trees infected). Fuller and Hostetler (1980) found marked differences between understory vegetation in lodgepole pine and frequency and abundance of dwarf mistletoe (table 3). Unfortunately, when that study was made, habitat type classifications had not been completed for the lodgepole pine forests in Colorado.

The use of the habitat type classification system of vegetation has increased greatly in the past decade in the Rocky Mountains. A habitat type is usually defined as a unit of land capable of producing a certain plant community at climax (Daubenmire and Daubenmire

Table 3.—Frequency and average mistletoe rating for lodgepole pine dwarf mistletoe by understory vegetation; based on 277 plots from Colorado (from Fuller and Hostetler 1980).

Predominant understory vegetation	No. of plots	% of plots with dwarf mistletoe	Average mistletoe rating
Shepherdia canadensis	12	50	1.3
Vaccinium scoparium	90	30	1.1
Juniperus communis	31	35	1.1
Arctostaphylos uva-ursi	41	23	1.0
Arnica cordifolia	12	33	1.0
Grasses (no shrubs)	45	20	0.7

1968). Although a given habitat type may support several seral plant communities, the final stage of plant succession will be a specific climax community. Thus, the habitat type system uses climax plant communities as an integrating indicator of the environmental conditions that influence plant reproduction, competition, and community development (Steele et al. 1981). The earliest study to compare lodgepole pine dwarf mistletoe in various habitat types was by Roe and Amman (1970), who examined 42 stands in the three main lodgepole pine habitat types in western Wyoming (Yellowstone and Teton National Parks, Bridger and Teton National Forests) and southeastern Idaho (Targhee National Forest):

Habitat type	Mean stand dwarf mistletoe intensity[2]
Abies lasiocarpa/Vaccinium scoparium	2.5
Abies lasiocarpa/Pachystima myrsinites	1.9
Pseudotsuga menziesii/Calamagrostis rubescens	1.6

A much more refined habitat type classification system for this area has since been developed by Steele et al. (1983). The habitat types cited by Roe and Amman (1970) are so broad that they cannot be correlated directly with the habitat type classes under the revised system. However, the *Pseudotsuga menziesii/Calamagrostis rubescens* habitat type, which had the least infection, probably has the lowest lodgepole pine growth potential of the three habitat types examined (R. Steele, personal communication, 1985).

Mauk and Henderson (1984), who developed a habitat type classification for northern Utah, included an evaluation of dwarf mistletoe for lodgepole pine in the Uinta Mountains. They recognized 26 habitat types that support lodgepole pine, 10 of which had dwarf mistletoe. The four types where infection was highest were: *Pinus contorta/Arctostaphylos uva-ursi* habitat type; *Abies lasiocarpa/Vaccinium scoparium* habitat type, *Carex geyeri* and *Vaccinium scoparium* phases; and the *Pinus contorta/Vaccinium caespitosum* community type (c.t.). The four types with heavy infection had a slightly lower average lodgepole pine site index [36 feet (11 m) at age 50] than the mistletoe-free types [39 feet (12 m) at age 50], but the data were so variable that the differences were not significant.

Wirsing (1973) studied habitat types in the Medicine Bow National Forest in southeastern Wyoming and found that dwarf mistletoe in lodgepole pine was more common in the *Pinus contorta/Carex geyeri* c.t. than in the more mesic *Pinus contorta/Vaccinium scoparium* c.t. Oswald (1966) noted that dwarf mistletoe was abundant in all four lodgepole pine communities recognized in the forested moraines of the valley floor in Grand Teton National Park, Wyoming.

No quantitative studies on the effects of dwarf mistletoe in various lodgepole pine habitat types and community types have been made. However, observations suggest that there are marked differences, such as have been documented for other host/parasite combinations. For example, the effects of heavy infection [dwarf mistletoe infection classes 5–6 (Hawksworth 1977)] by Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) on 10-year radial growth increment in the Southwest ranged from 24% to 75% in different habitat types (Mathiasen and Blake 1984).

Such studies are urgently needed for lodgepole pine in the Rocky Mountains. However, caution is advised in attempting to relate mistletoe occurrence to habitat types because of many other factors that may affect mistletoe distribution and abundance, especially past management practices, fire history, stage of succession, and topography.

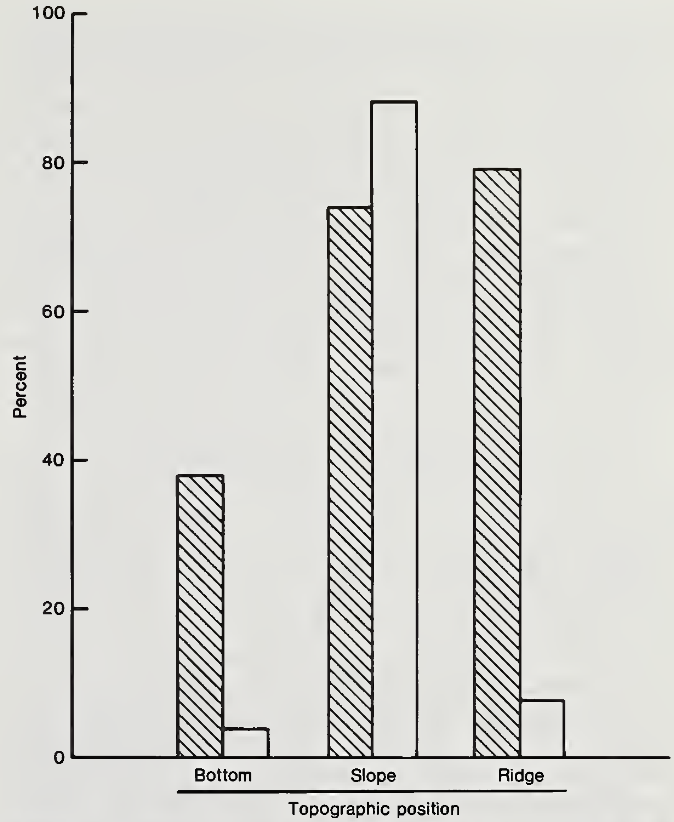


Figure 10.—Distribution of lodgepole pine dwarf mistletoe in relation to topographic position. Solid bars show incidence of dwarf mistletoe in each position. Open bars show distribution of plots in the three positions. Based on 426 plots in Colorado and Wyoming (Hawksworth 1958a).

Topography

Little information is available on the relationship of topography and lodgepole pine dwarf mistletoe.

Arceuthobium americanum is typically most abundant on ridges, but ridge sites occupy a relatively small proportion of the lodgepole pine area. Figure 10 shows the frequency of *A. americanum* in 426 lodgepole pine plots in the Roosevelt National Forest, Colorado, and the Medicine Bow and Bighorn National Forests in Wyo-

[2]Based on a 4-class rating system: 1 = no dwarf mistletoe, 2 = less than one-third of trees infected, 3 = one-third to two-thirds of trees infected, and 4 = more than two-thirds of trees infected.

ming. No studies have been reported on the relationships of lodgepole pine dwarf mistletoe and steepness of slope or aspect.

Elevation is the one physical site factor for which a considerable amount of information is available for lodgepole pine dwarf mistletoe (Hawksworth 1956, Williams et al. 1972). *A. americanum* ranges from as low as 700 feet (215 m) in northern Alberta to as high as 11,000 feet (3,350 m) in central Colorado. Hawksworth (1956) showed that there was a mistletoe-free zone of about 500 feet (150 m) in elevation just below the upper limits of the commercial lodgepole pine zone in the Rocky Mountains. The upper limits of *A. americanum* are about 9,000 feet (2,740 m) in northern Wyoming, and 10,000 feet (3,050 m) in northern Colorado (fig. 11).

Hawksworth and J. G. Laut (unpublished data, 1986) studied the reasons for the mistletoe-free zone in northern Colorado by transplanting mistletoe-infected lodgepole pines into the zone. After nearly 20 years, the mistletoe plants survived vegetatively and flowered, but fruits did not mature. The growing season at this elevation is apparently not long enough for the fruits to mature before the killing frosts in the autumn.

In a laboratory study, Baranyay and Smith (1974) found that *A. americanum* fruits exposed to 3.9° C for 2 to 5 hours were permanently damaged, and no seed dispersal occurred. Becwar et al. (1982) studied the cold-hardiness of dwarf mistletoe shoots and seeds, including *A. americanum*. Lodgepole pine dwarf mistletoe seeds avoided freezing damage by deep undercooling to about −35° C. Seeds cooled to −40° C were killed; however, vegetative shoots of this mistletoe survived cooling to −70° C.

Site Factors

No studies have been made to correlate incidence or abundance of lodgepole pine dwarf mistletoe with site quality in the Rocky Mountains. However, Hadfield (1977) found no direct relationship between site and dwarf mistletoe frequency in eastern Oregon or eastern Washington; dwarf mistletoe was most frequent in sites 65 to 75 feet, and least in stands over site 85 (height at base age 100 years).

Site index (feet)	Frequency of dwarf mistletoe (%)
<65	35
65–75	51
75–85	33
>85	20

Hawksworth and Graham (1963) measured the amount of mistletoes in young lodgepole pines adjacent to an infected overstory in the central and northern Rocky Mountains. They found a marked relationship between the abundance of dwarf mistletoe and height of the dominant trees in the young stand. Stands were classed as above or below average based on height of dominant trees: 6 feet (1.8 m) for stands 5–12 years old, 8 feet (2.4 m) for stands 13–19 years old, and 12 feet (3.7 m) for stands 20–28 years old. The percentage of trees infected, with mean and standard errors, were:

Tree height and age class	No. plots	% of trees infected
Above average:		
5–12 years	9	3.5 ± 2.5
13–19 years	12	14.5 ± 4.2
20–28 years	6	45.0 ± 10.4
Below average:		
5–12 years	15	0.4 ± 0.3
13–19 years	12	6.7 ± 1.8
20–28 years	6	9.7 ± 1.1

For reproduction at a given age, the proportion of trees infected was significantly higher for the plots with the tallest trees. Also, within a stand of reproduction, the tallest trees were usually infected first, presumably because they present more exposed target area. The percentage of plots with dwarf mistletoe was greater on the plots with above-average height growth, particularly in the younger stands. In the 5- to 12-year age class, the parasite occurred on 67% of the above-average plots, but on only 27% of the below-average plots. Thus, the evidence is strong that reproduction on good sites adjacent to an infected overstory is more prone to infection.

Our observations indicate that dwarf mistletoe occurs on essentially all sites in the central and northern Rocky Mountains (site indices at base age 100 from <30 to >95 feet (<9 to >29 m), although volume loss attributed to the parasite is less on better sites. Additional studies are needed to quantify the relationship of site factors to incidence and severity of lodgepole pine dwarf mistletoe.

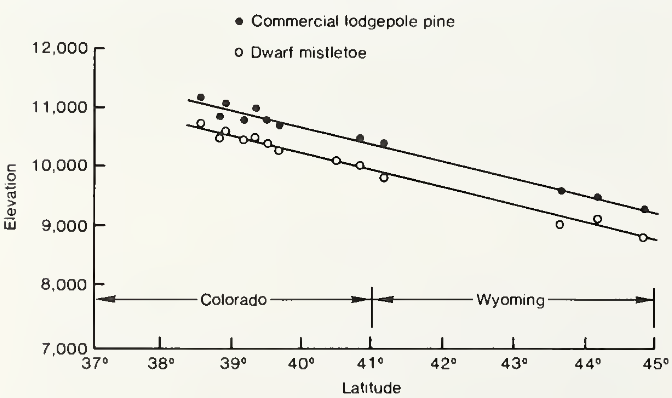


Figure 11.—The upper altitudinal limits of commercial lodgepole pine and dwarf mistletoe from central Colorado to northern Wyoming. The mistletoe-free zone averages about 500 feet in height. Updated from Hawksworth (1956).

Fire History

Wildfires have been most important in determining the present distribution of lodgepole pine dwarf mistletoe, because fire is the only effective natural control agent (Alexander and Hawksworth 1975, 1976, 1986). Little is known on the direct effects of smoke on dwarf mistle-

toes, but Zimmerman and Laven (1987) found that exposure of lodgepole pine dwarf mistletoe seeds to forest-fuel smoke for 60 minutes or longer inhibited germination but that exposure up to 30 minutes slightly increased germination.

Fire is particularly important for this dwarf mistletoe, because the development of most lodgepole pine forests has been fire-dependent. The many interrelated factors that influence fire cycles in lodgepole pine are summarized by J. K. Brown (1975). These include fuel build-up, mountain pine beetle epidemics, and dwarf mistletoe effects (fig. 12). Fire has played a major role in the determination of the present mistletoe distribution patterns of lodgepole pine and its mistletoe. For example, Baranyay (1972) stated that dissimilarities in fire history are the primary reason why there is much more dwarf mistletoe in lodgepole pine in the upper foothills and east slope Rockies forest types than in the lower foothills of Alberta. In the lower foothills, wildfires during the past 100 years were very extensive and complete. The young lodgepole pine stands that developed in these burns are relatively free of mistletoe. In the other two forest types, however, variations in topographic and forest conditions prevented the development of large conflagrations. Many residual mistletoe-infected trees survived and infected the young stands that developed after wildfires.

Surveys by Hawksworth (1958a) show that dwarf mistletoe is considerably less in regenerated burns than in adjacent virgin or cut-over stands:

Stand condition	Percent of stands	
	Infested	Heavily infested
Virgin	49	28
Partially cut	66	41
Regenerated burns	24	5

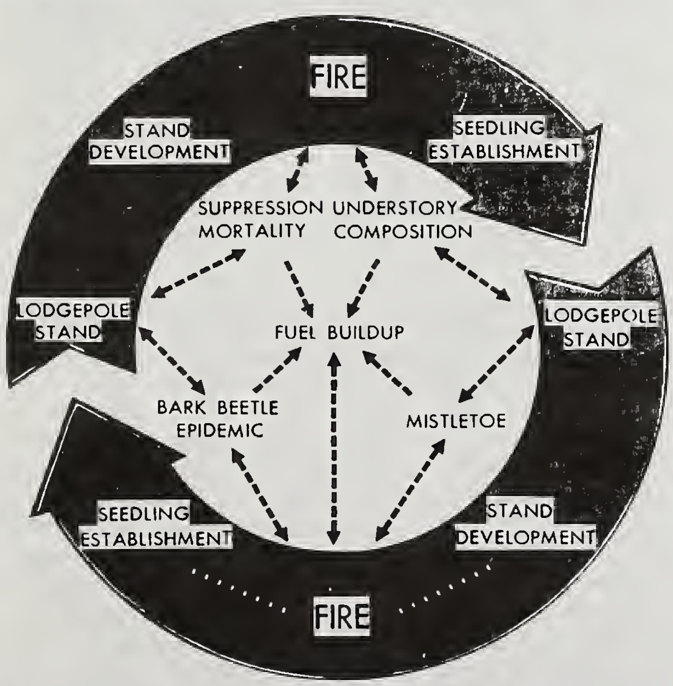


Figure 12.—The many related factors influencing the fire cycle in lodgepole pine forests (from J. K. Brown 1975).

Lodgepole pine reproduction in clearcuts or burned areas in the northern Rocky Mountains of Idaho and Montana is generally uninfected or only lightly infected by dwarf mistletoe (LeBarron 1952). Lotan (1975) stated that fire provides a self-correcting check on insects and diseases, and noted the lodgepole pine area burned by the large Sleeping Child fire in Montana is likely to be relatively free of mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoe for decades. Similarly, Taylor (1969) found that infection in regenerated lodgepole pine burns in Yellowstone National Park was relatively low. The slow reinvasion of dwarf mistletoe from adjacent unburned stands was correlated with time since the burn.

Years since burn	% of lodgepole pines infected
7	0
13	0
25	0
57	1
111	10
ca. 300	36

Lodgepole pine dwarf mistletoe usually is more common on ridge and slope sites than in bottom sites (Hawksworth 1958a). This may be, at least partly, a result of different intensities of wildfires and tree survival at the different sites, because ridge stands tend to be more open with less fuels.

Immature lodgepole pine stands infested by dwarf mistletoe have more dead material on the ground, more stems, and more foliage near the ground than comparable uninfested stands (Alexander 1979, Hawksworth and Hinds 1964). J. K. Brown (1975) stated that dwarf mistletoe often adds to the ground fuel, and also that witches' brooms enhance vertical fuel continuity and, thus, increase the likelihood of ground fuels creating a "fire ladder" to burn individual tree crowns. The witches' brooms also tend to trap fallen needles, thus increasing the vertical scattering of fine fuels which are ideally situated for optimal flammability.

In a broad, ecological sense, wildfires may tend to increase certain mistletoe-susceptible seral tree species, such as lodgepole pine and jack pine. For example, the climax spruce-fir (*Picea engelmannii-Abies lasiocarpa*) forests of the Rocky Mountains are generally resistant to dwarf mistletoes; the seral lodgepole pine, which frequently replaces spruce-fir on burned sites, is very susceptible to dwarf mistletoe (Kuijt 1955, Hawksworth 1975). Whether or not mistletoe increases in the seral stand, however, depends on the availability of infection sources. If no infected lodgepole pines occur in the area, then young lodgepole pine stands will remain free of dwarf mistletoe. An important role of fire in relation to succession seems to be the maintenance of seral stands by intermittent fire. Dwarf mistletoe seed sources are not eliminated; therefore, the disease is maintained in subsequent seral stands.

Control of wildfires over the past few decades may have increased the amount of dwarf mistletoe in lodge-

pole pine forests (Alexander and Hawksworth 1975). Zimmerman and Laven (1984) quantified this in one area in central Colorado and showed the fire frequency peaked between 1860 and 1890 (long before fire control efforts were initiated) and has declined steadily since then. Concurrently, dwarf mistletoe increased from very low levels before 1900 to where essentially every stand is infested to some degree today.

HOST EFFECTS

Dwarf mistletoes affect their hosts in several ways, some of which have not been quantified. Heavily infected trees show a marked decline in vigor, as evidenced by upper crowns that are more open and have smaller, yellow-green needles. The rates of height and diameter growth decline, seed and cone production is reduced, and eventually trees start to die back from their tops. Premature death follows, usually aided by secondary bark beetles.

Vigor

Hawksworth (1958a) quantified the relationship of dwarf mistletoe to vigor of lodgepole pine. He compared the board foot volume in infected and uninfected trees in the four vigor classes as defined by Taylor (1939) (fig. 13):

Class A.—Crown area: 30% or more of the "extreme maximum" outline of vigor class A. Crown length: 50% or more of the bole length. Crown vigor: dense, full, of good color, and pointed.

Class B.—Crown area: usually more than 30% but less than 50% of the "extreme maximum" outline of vigor class A. Crown length: usually more than 50% but less than 60% of the bole length. Crown vigor: moderately dense, of good color, pointed, or slightly rounded.

Class C.—Crown area: 17% to 30% of the "extreme maximum" outline of vigor class A. Crown length: 40% to 50% of the bole length except for trees with distinctly better than average vigor when a minimum of 20% of the bole length is sufficient. Crown vigor: sparse, bunchy, color poor, never pointed.

Class D.—All live trees of poorer vigor than class C. Includes trees with class A, B, or C outlines but with dying or multiple tops.

A summary of the percentage of tree volume in each dwarf mistletoe or vigor class in virgin and cutover stands is given in figure 14. Volume in trees of highest vigor (class A) was much greater in uninfected than infected trees in both stand types. Thirty-three percent of the volume was in infected trees in the better vigor classes (A and B) compared to 56% for uninfected trees in virgin stands.

A more detailed analysis from the data collected by Hawksworth (1958a) was made to determine the relationship between vigor rating and dwarf mistletoe intensi-

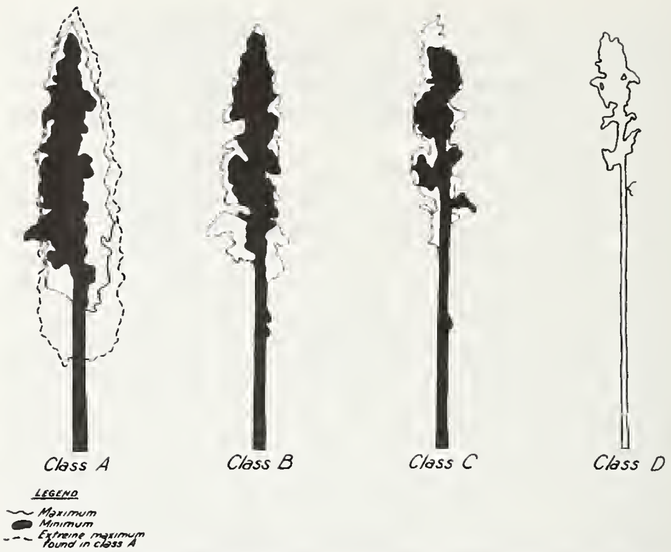


Figure 13.—Lodgepole pine tree vigor classes (Taylor 1939).

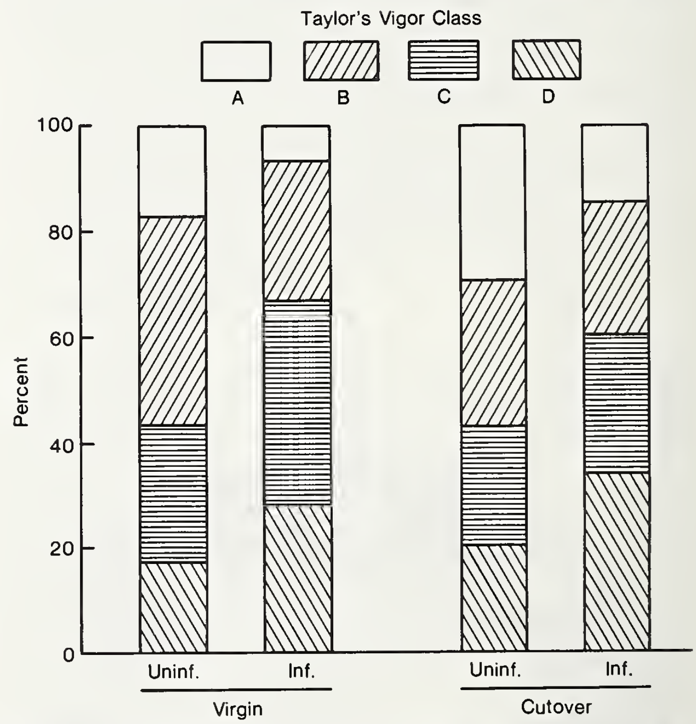


Figure 14.—Distribution of board-foot volume in 2,610 trees by Taylor vigor class for uninfected (uninf.) and infected (inf.) lodgepole pines (>10 inches d.b.h.) in virgin and cutover stands in Colorado and Wyoming (Hawksworth 1958a).

ty. The results (fig. 15) show that trees with higher mistletoe intensities have lower vigor ratings. For example, about 20% of the trees in infection classes DMR 0–2 were in vigor class A. This dropped to 15%, 9%, 3%, and 0% for trees in infection classes 3, 4, 5, and 6, respectively. Similarly, trees of the poorest vigor (class D) averaged about 20% for trees in infection classes 0–3, but this increased for trees in infection classes 4, 5, and 6 to 26%, 28%, and 66%, respectively.

Schaffer et al. (1983a) used a Shigometer to measure the electrical resistance of lodgepole pines of various

dwarf mistletoe intensities (6-class system) and vigor classes. Vigor was subjectively rated into three classes:

Good: normally colored foliage, full crown.
Fair: foliage color or crown density intermediate.
Poor: off-color foliage or open crown.

Electrical resistance was significantly related to vigor class (good: 16.3 ± 0.4 k-ohms; fair: 21.9 ± 1.2 k-ohms; and poor: 30.0 ± 3.6 k-ohms). Only the most heavily infected trees (class 6) had a significantly higher electrical resistance than the healthy or less severely infected trees.

Diameter Growth

Hawksworth and Hinds (1964) determined the effects of dwarf mistletoe on diameter growth on 25 even-aged plots in Colorado that ranged from 50 to 150 years old. Reduction in diameter growth was significantly correlated to time since infection: for the first 70 years after infection, reduction in diameter growth averaged about 5% per decade. That is, trees that had been infested for 70 years showed a radial growth of about 65% of that of comparable uninfected trees (fig. 16).

Baranyay and Safranyik (1970) conducted the only tree-dissection study to determine growth rates of mistletoe-infected lodgepole pines. They dissected five trees in Alberta: two healthy, one lightly infected, and two heavily infected (classes 2 and 3).[3] Trees were measured at stump height (1 foot) and at 8-foot intervals to the top. Radial growth in lightly infected trees was not significantly different than the uninfected trees, but the two

[3] *Based on a 4-class rating system: 0 = healthy; 1 = light branch infections, less than 50% of the crown infected; 2 = heavy branch and stem infections, more than 50% of the crown infected; and 3 = witches' brooms, branch and stem infections, more than 50% of the crown infected.*

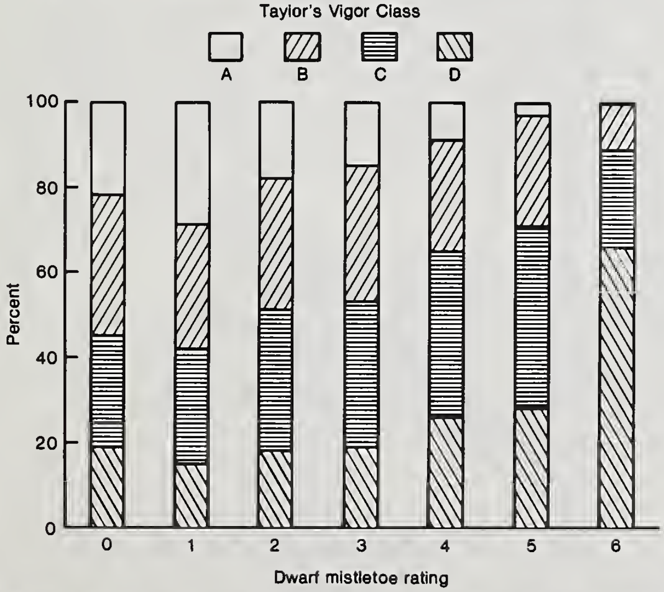


Figure 15.—Relationship between dwarf mistletoe intensity and Taylor vigor class. Based on 2,610 mature trees (>10 inches d.b.h.) in Colorado and Wyoming. Data from survey reported by Hawksworth (1958a).

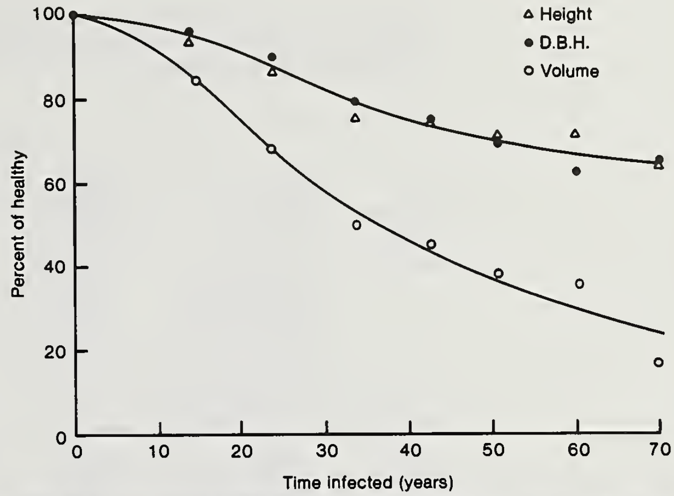


Figure 16.—Relative height, d.b.h., and cubic foot volume of dominant and codominant lodgepole pines in relation to time since infection. Based on 133 plot pairs on 25 transects in Colorado (Hawksworth and Hinds 1964).

heavily infected trees had significantly ($P = 0.01$) slower growth rates. Although Baranyay and Safranyik (1970) did not summarize their data on radial growth reduction in relation to tree height, their diagrams suggest that the effects of mistletoe are slightly more pronounced with increasing height above the ground.

Data from more than 3,000 trees in 25 even-aged plots in Colorado (Hawksworth and Hinds 1964) were analyzed for radial growth rate at d.b.h. in comparison with dwarf mistletoe intensity, crown class, and stand density (table 4). The radial growth rate in dominant trees decreased markedly in heavily infected (classes 5 and 6) trees. Growth in class 5 and 6 trees was 75% and 54%, respectively, of that in class 0–3 trees in open stands compared to 90% and 76% for dense stands, respectively. The relative effects of dwarf mistletoe were more pronounced in open than in dense stands; growth rates of class 4 trees were less in open stands (89%) than in dense ones (96%). In open stands, the percentage losses were similar in dominant, codominant, and intermediate, but less in suppressed trees. However, in dense stands, losses were most marked in codominant and intermediate trees, less so in suppressed, and least in dominant trees. For all 3,015 trees analyzed, growth reduction in relation to that in classes 0–3 by dwarf mistletoe intensity was:

Class 4	6%
Class 5	20%
Class 6	41%

A general equation for estimating the difference in 10-year radial growth in even-aged lodgepole pine stands (Myers et al. 1971) is:

$$Y = 1.0222\,X_1 + 0.0151X_2 - 1.2417\,\log^{10} X_3 + 2.1450$$

where

Y = 10-year radial growth difference from healthy stands,
X_1 = d.b.h. at start of period,
X_2 = site index (feet at base age 100), and
X_3 = basal area (square feet) per acre.

Table 4.—Ten-year radial growth rates in open (<1000 trees/acre) and dense (>1000 trees/acre) stands in relation to dwarf mistletoe intensity and crown class; based on 25 even-aged plots in Colorado and Wyoming.

Density	Crown class	No. of trees	Growth (in.) for DMR class 0-3	10-yr radial growth rate expressed as a percentage of class 0-3 for DMR class 4	5	6
Open	Dominant	132	0.35	89	75	54
	Codominant	106	0.29	100	83	52
	Intermediate	659	0.25	99	90	52
	Suppressed	217	0.14	92	82	65
Total and unweighted means		1,114	0.26	95	82	56
Dense	Dominant	179	0.21	96	90	76
	Codominant	206	0.20	67	63	52
	Intermediate	605	0.14	101	84	56
	Suppressed	911	0.06	109	77	60
Total and unweighted means		1,901	0.15	93	78	61

For stands with an average stand dwarf mistletoe rating of less than 3.9, no adjustment is needed.

In summary, low intensities of dwarf mistletoe have no measurable effect on radial growth. As a rule, the threshold level for growth reduction seems to be class 3, or when about one-half of the crown becomes infected. In some instances (e.g., for intermediate or suppressed trees in dense stands), growth loss may be detected only in class 5 and 6 trees.

Effects of dwarf mistletoe on average stand diameter for lodgepole pine stands of various intensities of infection using the RMYLD program were determined by Van der Kamp and Hawksworth (1985). For this analysis, a site index of 60 feet (18.3 m), thinning interval of 20 years, and growing stock level (GSL) of 100 ft^2/acre (23 m^2/ha) were used. GSL is defined as the residual square feet of basal area where average stand diameter is 10.0 inches or more (Alexander and Edminster 1980). As shown in figure 17, infection class DMR 1 has no measurable effect, but higher ratings have progressively more effect so that, by class DMR 5, decreases in growth were significant.

Height Growth

Despite all the research on lodgepole pine dwarf mistletoe, relatively little quantitative data are available on the effects of the parasite on height growth of the host. Weir (1916) measured 50 infected and 50 uninfected 60- to 65-year-old lodgepole pines in northern Idaho and eastern Washington. Uninfected trees averaged 48.5 feet (14.8 m) high, compared to 35.2 feet (10.7 m) for infected trees, a difference of 27%.

Dwarf mistletoes generally have more effect on height growth than on diameter growth. However, Hawksworth and Hinds (1964) (see previous section), in a study of 25 even-aged lodgepole pine stands in Colorado and Wyoming, found that growth retardation in height and diameter were about the same (i.e., about 0.5% per year).[4]

Baranyay and Safranyik (1970) found no effect of light infection on height growth in Alberta. However, heavily infected trees were slightly shorter in a dry, but not on a wet, site.

Meyers et al. (1971) developed the following relationship between 10-year reduction in height growth in

[4]*Erroneously reported by Hawksworth and Hinds (1964) as 0.7% per year.*

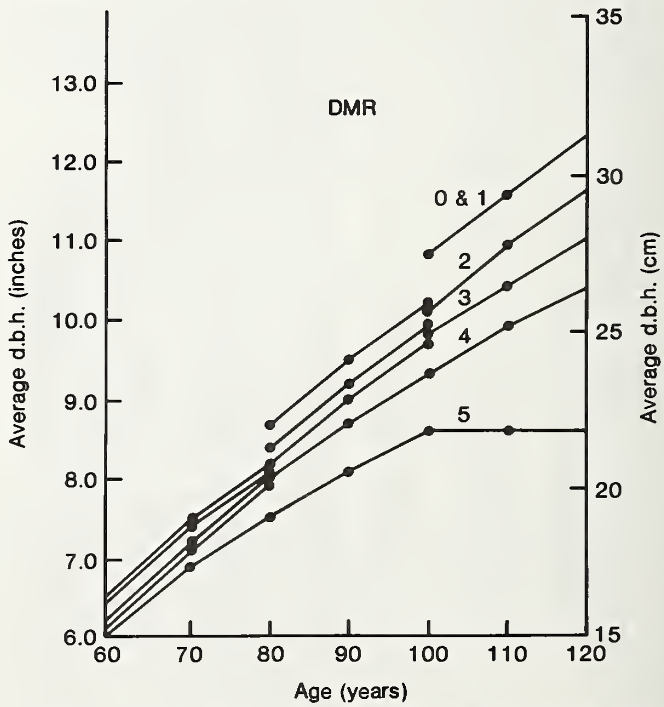


Figure 17.—Relationship between diameter growth and dwarf mistletoe rating (DMR). Mistletoe ratings at age 60. Site index 60 feet (18.3 m), thinning interval 20 years, and growing stock level 100 ft^2/acre (23 m^2/ha.)

dominant and codominant trees, and stand dwarf mistletoe rating [based on the data of Hawksworth and Hinds (1964) from 25 stands in Colorado]:

$$\hat{Y} = 100 - 1.65 X_1^3$$

where

$\hat{Y}$ = percent reduction in height growth compared to mistletoe-free trees, and
X_1 = dwarf mistletoe rating.

This is equivalent to:

DMR	10-year percent height growth reduction
0–1	0
2	2
3	8
4	18
5	35
6	60

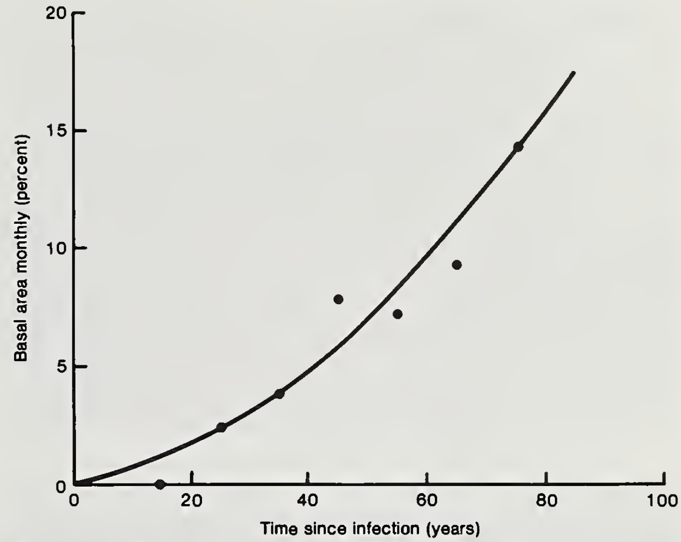


Figure 18.—Basal area mortality for previous 10 years in infested stands in relation to uninfested stands. Data from 25 even-aged stands in Colorado (Hawksworth and Hinds 1964).

Mortality

There is considerable literature on the deleterious effects of lodgepole pine dwarf mistletoe on yields, but most studies do not separate losses resulting from growth reduction from those caused by mortality.

Hawksworth (1958a) compared mortality in mistletoe-free stands and those with various intensities of dwarf mistletoe in Colorado and Wyoming. Recent mortality was greater in infested than in uninfested stands. To compare infested and uninfested stands, recent mortality was calculated as the volume of standing dead trees with bark intact[5] expressed as a percentage of the gross volume in both living and dead trees. Recent mortality in uninfested virgin stands was 800 board feet per acre, while that in infested stands was 1,020 board feet, or 1.3 times, greater (table 5). The difference between percent mortality in infested and uninfested stands is greater than 1.3, since past mortality and growth reduction caused by the parasite lowered the gross volume in infested areas. Mortality in cutover stands was 490 board feet per acre (8.8% of gross volume) in uninfested plots and 560 board feet (12.5% of gross volume) in plots with dwarf mistletoe.

Hawksworth (1958a) found that stand density in uninfested pole stands was about 1.5 times that in infested stands. In large poles (those over 5.6 inches d.b.h.), mortality in infested stands was five times greater than in mistletoe-free stands. However, in small poles where suppression is the predominant mortality factor, the proportion of dead trees in infested and uninfested stands was about the same.

In a study of 25 even-aged lodgepole pine stands in Colorado and Wyoming, Hawksworth and Hinds (1964) found that mortality was directly related to time since dwarf mistletoe infection began (fig. 18). Basal area in dead, standing trees as a percentage of total basal area in living plus dead trees increases dramatically with time since infection from less than 5% for stands infested for about 40 years to 15% in stands infested for 80 years.

Baranyay and Safranyik (1970) studied five infested lodgepole pine stands in Alberta and found that recent

[5]*This approximates mortality during the previous 10 years.*

Table 5.—Effect of dwarf mistletoe on volume and recent mortality in merchantable lodgepole pine in virgin stands, based on 151 plots in Colorado and Wyoming (Hawksworth 1958a).

Stand type	Plot basis	Gross volume per acre			Mortality[1]
		Living	Dead	Total	
	no.	*board-feet*			%
Not infected	44	10,930	800	11,730	6.8
Infected:					
Light (DMR 1-2)	23	10,100	1,180	11,280	10.5
Moderate (DMR 3-4)	36	7,990	1,150	9,140	12.6
Heavy (DMR 5-6)	48	5,280	850	6,130	13.8
Total or average	107	7,230	1,020	8,250	12.4

[1]*Dead standing trees with bark intact—approximate mortality during previous 10 years.*

mortality (dead standing trees with bark intact) was related to time since infection and was higher on dry than on wet sites (table 6).

General equations for estimating 10-year mortality in even-aged lodgepole pine stands in the central Rocky Mountains are given by Myers et al. (1971). For stands with less than 1,000 stems/acre:

$$\hat{Y} = -0.663 + .0381\ X$$

for stands with greater than 1,000 stems/acre,

$$\hat{Y} = -0.864 + .0328\ X$$

where

$\hat{Y}$ = percent tree mortality in 10 years, and
X = stand DMR.

These equations apply only to stands with an average DMR of 3.9 or more; below that level, mistletoe-caused mortality is negligible.

Volume Growth

Because of reduced rates of height and diameter growth in infected trees and increased rates of mortality, volume growth in infested stands is typically less than in comparable mistletoe-free stands. The actual reduction depends on several factors, primarily intensity of infection, site index, and stand density.

To enable forest managers to predict yields in healthy and mistletoe infested stands, the RMYLD simulation program was developed for lodgepole pine for the central Rocky Mountains by Edminster (1978). This program makes it possible to estimate yields in infested stands with various stand management alternatives (thinning intensity, thinning intervals, rotation ages) (appendix I).

The only other lodgepole pine growth and yield model that considers dwarf mistletoes is Schmitt and Wittala's (1983) modification of Dahm's (1983) yield tables for central Oregon.

A comparison of estimated yields (using the RMYLD system) in lodgepole pine of three growing stock levels (GSL) 60, 100, and 140 ft^2/acre (13.8, 23.0, and 32.1 m^2/ha) and various intensities of DMR's appear in table 7 (Van der Kamp and Hawksworth 1985). Intensity of infection is based on the 6-class (DMR) rating system (Hawksworth 1977). For the comparisons, these conditions are assumed: present age, 60 years; 600 trees/acre (1,483 trees/ha); site index, 60 feet (18.3 m); average d.b.h., 6.0 inches (15.2 cm); thinning interval, 20 years. Projections are made for a 60-year period on to rotation age 120. Results show that, for healthy and lightly infested stands (up to DMR 2), anticipated yields increase with growing stock levels. For stands with a DMR 3 or 4 at the beginning of the period, there is little relationship between GSL and yields, and for heavily infested (class 5) stands, yields decrease with increasing GSL. For example, in DMR class 5 stands with a GSL of 60 ft^2, an-

Table 6.—Mortality in five lodgepole pine stands in Alberta in relation to stand factors and dwarf mistletoe (adapted from Baranyay and Safranyik 1970).

Stand	Stand age	Time infected	Trees infected	Mortality due to mistletoe[1]
	yr	yr	%	%
Dry site 1	37	28	48	0
Dry site 2	59	41	77	11
Dry site 3	86	45	58	10
Dry site 4	117	58	62	26
Wet site 1	86	50	35	4

[1] *Percent of dead trees on infested plot, less the percent of dead trees on a control plot in each stand.*

Table 7.—Estimated total yields (from RMYLD projections) at age 120 (in merchantable cubic feet per acre) in Rocky Mountain lodgepole pine. [Stands now 60 years old; site index 60, thinning interval 20 years (Van der Kamp and Hawksworth 1985.)]

Stand DMR at age 60	Growing stock level: 60		100		140	
	Yield	% of healthy stand	Yield	% of healthy stand	Yield	% of healthy stand
0	3,970	100	5,180	100	6,270	100
1	3,930	99	5,120	99	6,170	98
2	3,640	92	4,200	81	4,390	70
3	2,980	75	3,160	61	3,130	50
4	2,170	55	2,220	43	2,240	36
5	1,420	36	1,110	21	860	14

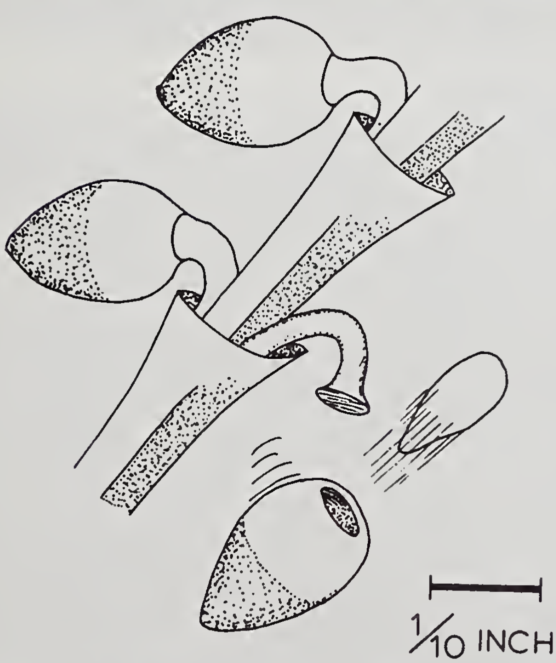
Plate I. Dwarf mistletoe plants, fruits, and seeds.

1. Female dwarf mistletoe plant.

2. Male dwarf mistletoe plant in flower.

3. Closeup of female plant with mature fruits.

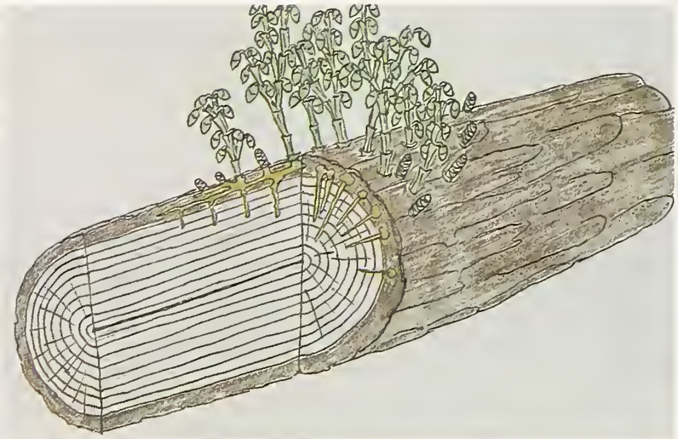
4. Closeup of distal portion of male plant with open flowers.



5. Diagram showing seed expulsion from mature fruit.

6. Photograph of seed expulsion taken at 5 millionths of a second.

Plate II. Dwarf mistletoe infections.



1. Diagram of cross-section of pine stem showing dwarf mistletoe aerial shoots and the mistletoe root (endophytic) system in the cortex and in the xylem (the sinkers).

2. Cross-section of a mistletoe-infected lodgepole pine branch showing the mistletoe endophytic system in the cortex and the radial sinkers in the xylem.

3. Young dwarf mistletoe infection on a lodgepole pine branch showing a fusiform swelling and emerging shoots.

4. Dwarf mistletoe infection on the bole of a young lodgepole pine.

5. Swelling and distortion of the bole of lodgepole pine due to dwarf mistletoe. Such trees are unusable for most timber products.

6. Enlarged branches and bole swellings seriously reduce the merchantability of this lodgepole pine.

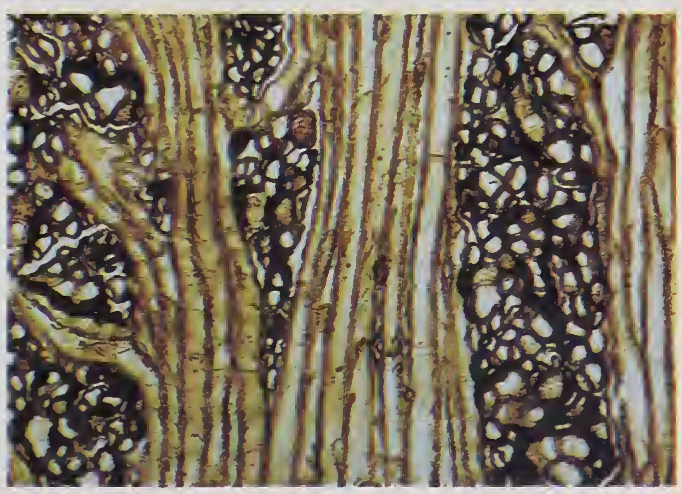
Plate III. Dwarf mistletoe effects on lodgepole pine.

1. Witches brooms are the most obvious symptom of dwarf mistletoe infection.

2, 3. These are "stimulation" brooms and are not caused by dwarf mistletoe. Stimulation brooms are frequent in residual lodgepole pines in cut-over areas. See text and Table 10 for details on how to distinguish the two types of brooms.

4. Lodgepole pines heavily infected by dwarf mistletoe typically start declining from the top, form spike tops, and are prematurely killed.

5. Tangential section of normal lodgepole pine wood.



6. Tangential section of lodgepole pine wood affected by dwarf mistletoe, showing the marked increase in ray volume (consisting of both mistletoe and host tissues) and shorter and distorted tracheids.

Plate IV. Biotic associates of lodgepole pine dwarf mistletoe.

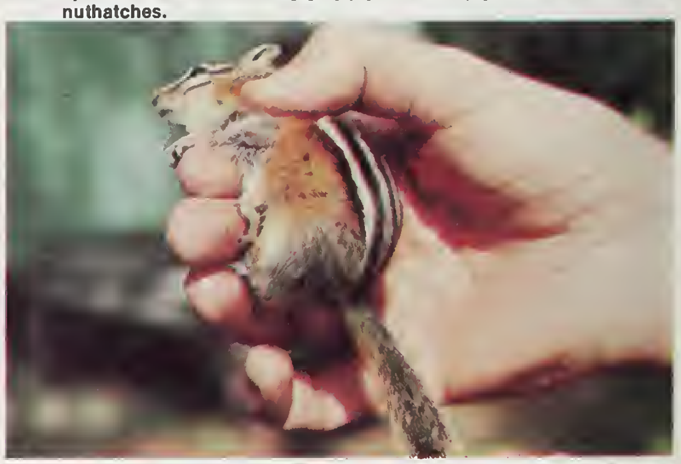
1. Aecia of the mistletoe rust, *Peridermium bethelii*, a unique fungus that is restricted to mistletoe-infected lodgepole pine. It frequently kills mistletoe-infected branches.

2. Larvae of the hairstreak butterfly, *Mitoura spinetorum*, feed exclusively on dwarf mistletoe shoots, including *Arceuthobium americanum* on lodgepole pine and kills many shoots in some years.

3. Red squirrels frequently feed on the bark of dwarf mistletoe-infected lodgepole pines.

4. Lodgepole pine dwarf mistletoe seeds have been found on at least 10 species of birds, including gray jay, Steller's jay (shown here), and nuthatches.

5. Lodgepole pine dwarf mistletoe seed on Steller's jay.



6. A few mammals also carry dwarf mistletoe seed as shown by this least chipmunk with two seeds (one on the tail and one on the left leg).

Plate V. Dwarf mistletoe-infested lodgepole pine stands.

1. Infected lodgepole pine stand being replaced by Engelmann spruce which is not attacked by lodgepole pine dwarf mistletoe.

2. Heavily-infested mature lodgepole pine stand showing high mortality and spike-topped trees.

3. Use of fire to replace heavily infested lodgepole pine stand.

4. Heavy dwarf mistletoe in lodgepole pine pole stand.

5. Dwarf mistletoe witches brooms frequently act as fire ladders to spread flames from ground fires up into the crowns.

6. Fire-killed dwarf mistletoe-infected lodgepole pine stand being replaced by healthy lodgepole pine reproduction.

Plate VI. Control of lodgepole pine dwarf mistletoe.

1. Application of Ethephon to limit dwarf mistletoe spread in a campground.

2. Typical dwarf mistletoe plant before Ethephon application.

3. The same plant 5 weeks application showing shoot abscission.

4. Trees heavily infected in the lower half of their crowns before broom pruning.

5. The same trees 6 years after broom pruning. Note the increase in crown density and vigor.

Plate VII. Silvicultural control of lodgepole pine dwarf mistletoe.

1. Residual infected trees in cut-over area. These will be removed when the new young stand is established.

2. Clearcut area in formerly heavily-infested lodgepole pine stand. To minimize dwarf mistletoe spread into the subsequent stand, the clearcut boundaries were placed in mistletoe-free parts of the stand.

3. A Marden Chopper that is used in clearcut areas to remove all residual trees, chop up slash, expose a mineral seed bed, and to scatter lodgepole pine seeds.

4. The same area as in 2 above, nine years after clearcutting showing a mistletoe-free, naturally established stand of lodgepole pine reproduction.

5. A dwarf mistletoe-infected lodgepole pine stand that has been commercially thinned by removing the most heavily infected trees.

6. Optimum silvicultural control in dwarf mistletoe-infested lodgepole pine stands involves application of various types of treatments to specific mistletoe and stand conditions. In this area the disease was so heavy in the stand in the foreground that it was clearcut, in the stand in the background, the disease was less severe so thinning was feasible.

ticipated yields are 36% of comparable healthy stands, but are only 14% for DMR class 5 stands with a GSL of 140 ft^2/ha. The same trend in mean annual increment is shown in figure 19.

The predicted merchantable cubic foot and metric volume from age 60 to 120 in stands with various mistletoe intensities is given in figure 20. The very light class infections (class 1) had no significant effect on yields, but all other infection classes do. Even stands with an intensity of DMR 2 at age 60 will have high infection levels (DMR 5+) by age 120.

Dwarf Mistletoe-Bark Beetle Relationships

Relationships between primary bark beetles (*Dendroctonus* spp.) and dwarf mistletoes are poorly understood (Stevens and Hawksworth 1984). In some beetle-dwarf mistletoe combinations, susceptibility of mistletoe-infected trees is increased; but most of the evidence for lodgepole pine indicates that mistletoe-infected trees are less susceptible to *Dendroctonus ponderosae* (McGregor 1978, Stevens and Hawksworth 1984). The primary reason for this seems to be that mistletoe-infected trees have thinner phloem (Roe and Amman 1970). However, Hawksworth et al. (1983) found little correlation between lodgepole pine phloem thickness and dwarf mistletoe intensity in Colorado. An exception is local bole infections that have thicker bark than adjacent, uninfected parts of the bole (McGregor 1978). In Colorado, at least, there seems to be little or no change in mountain pine beetle susceptibility resulting from mistletoe. Although the effect has not been quantified, the opening-up of stands by mortality caused by mountain pine beetle tends to increase spread and intensity of dwarf mistletoe in the residual trees (Wellner 1978).

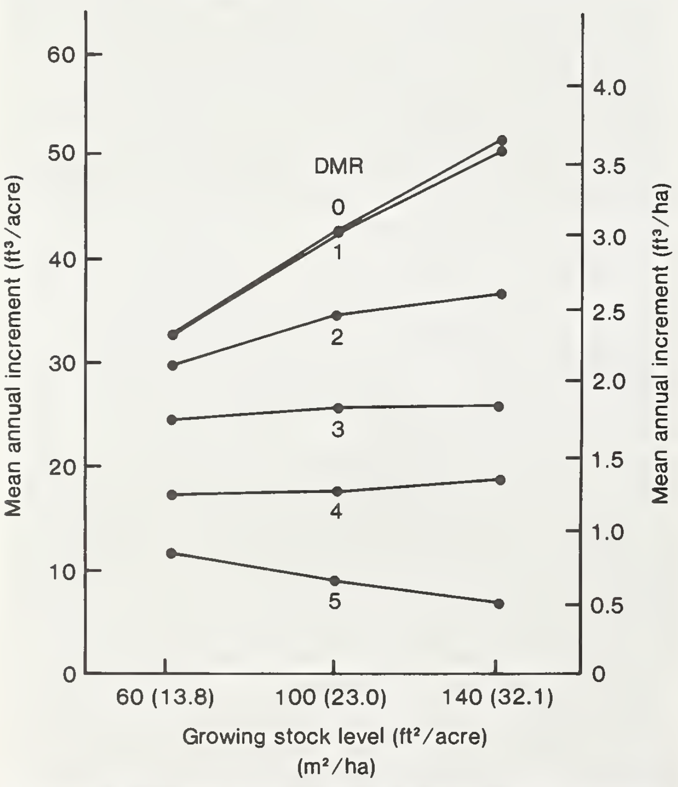


Figure 19.—Relationship of mean annual increment at rotation age (120 years) in relation to three growing stock levels based on six mistletoe rating classes at age 60. Based on site index 60 feet (18.3 m) and thinning interval 20 years (Van der Kamp and Hawksworth 1985).

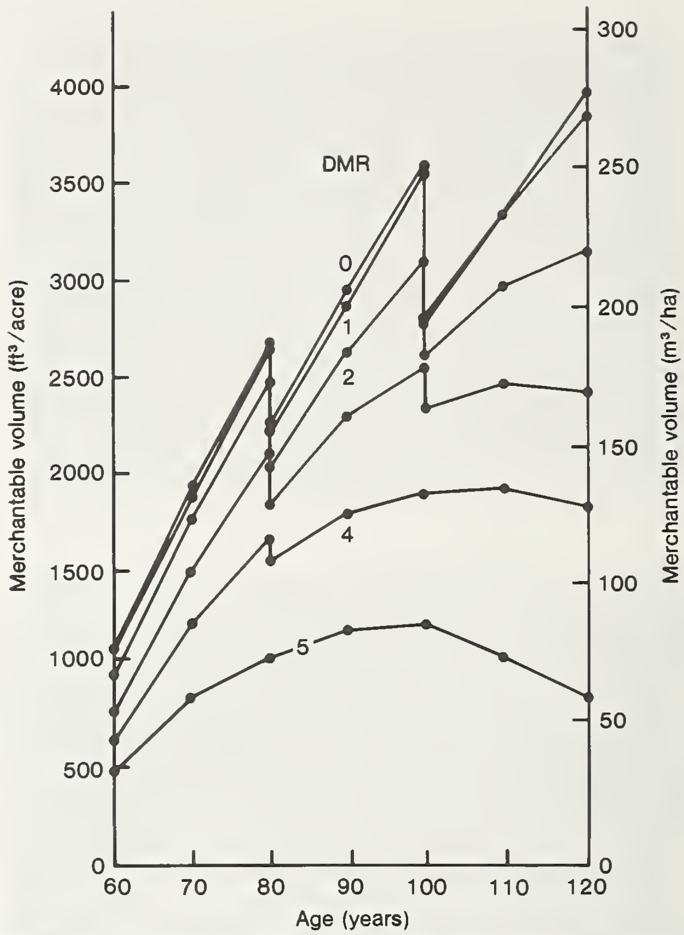


Figure 20.—Projected yields (merchantable cubic feet per acre and meters per hectare) in stands of various infection ratings at age 60. Site index 60 feet (18.3 m), thinning interval 20 years, and growing stock level 100 ft^2/acre (23.0 m^2/ha) (Van der Kamp and Hawksworth 1985).

Seed and Cone Production

Several observations that dwarf mistletoes adversely affect seed and cone production in lodgepole pine have been reported (Plate IV) (Bates 1930, Weir 1916); but only Schaffer et al. (1983b) provided quantitative data. Although they found a trend toward smaller cones, fewer cones per tree, fewer filled seeds, lower germination of filled seeds, and decreased seed size in heavily infested trees (DMR class 5 and 6), only the latter was significantly different (table 8).

Wood Quality

Dwarf mistletoes adversely affect lodgepole pine wood quality in several ways: (1) stems are often swollen and

Table 8.—Seed and cone production in lodgepole pine in relation to dwarf mistletoe intensity (from Schaffer et al. 1983b)

DMR infection class	No. of trees	Tree vigor[1]	Closed cone size[2]	Seed size[2]	Germinated filled seeds
			cm	*mm*	*no.*
0	10	1.7a[3]	2.9a	3.1a	35a
2-4	20	2.9b	2.8b	2.9b	30a
5-6	20	2.9b	2.8b	2.9b	20a

[1]*Vigor estimates based on color and density of needles (1 = dense, mostly green foliage; 2 = fairly dense, partially green foliage; and 3 = sparse, yellow-green foliage).*

[2]*Cone size = (length + width)/2; seed size = (length + width)^2.*

[3]*Numbers followed by the same letter are not significantly different (P = 0.05), Duncan's multiple range test.*

distorted so merchantability is reduced; (2) large knots caused by enlarged mistletoe-infected branches increase degrade of lumber; and (3) wood in infected trees, especially bole infections, is weakened because of a high proportion of ray tissues and shortened, distorted tracheids.

Piirto et al. (1974) found that the modulus of elasticity, modulus of rupture, and work to proportional limit were reduced not only in wood directly invaded by the mistletoe endophytic system, but even in non-infected wood in infected trees. They also found a higher specific gravity, higher percentage of alcohol-benzene extractives, and increased longitudinal shrinkage and increased microfibril angle in infected wood.

While the wood quality is adversely affected by dwarf mistletoe, the practical effects of the parasite on degrade in lodgepole pine lumber recovery are negligible (Dobie and Britneff 1975). A probable reason for this apparent anomaly is that the wood that is most affected is in the outer sapwood and tends to be removed in slabbing.

MANAGEMENT OF MISTLETOE-INFESTED STANDS

As previously discussed, the most important effects of *A. americanum* on its host are reduced growth and vigor and increased mortality. An estimate of commercial forest acreage infested and annual volume loss is presented in table 9. This discussion concentrates on silvicultural practices that can reduce the effects of the disease in forests managed primarily for fiber production and developed sites where tree cover and its condition are emphasized (Plates V, VI, and VII). Very little research has been conducted on the effects of the disease on non-commodity values, such as wildlife, recreation, watershed, and visual quality.

A summary of the options for managing commercial and recreational lodgepole pine forests infested with dwarf mistletoe is presented in figure 21. These options provide only general guidelines; decisions for actual treatments should be made on a stand-by-stand basis.

Management of Stands for Fiber Production

Dwarf mistletoes are most easily and economically treated by silvicultural practices. Dwarf mistletoe control needs to be an integral part of good forest management and practiced as a part of normal stand management activities (Alexander 1986, Alexander and Edminster 1980, Baranyay and Smith 1972, Dooling and Brown 1976, Schmidt and Alexander 1985, Wicker and Hawksworth 1988). Management of infested stands includes the detection, evaluation, prevention, and suppression of the disease. These activities must progress in a planned, timely manner for successful reduction of disease impact on the resource.

Several features of these parasites make them ideal candidates for cultural management (Johnson and Hawksworth 1985):

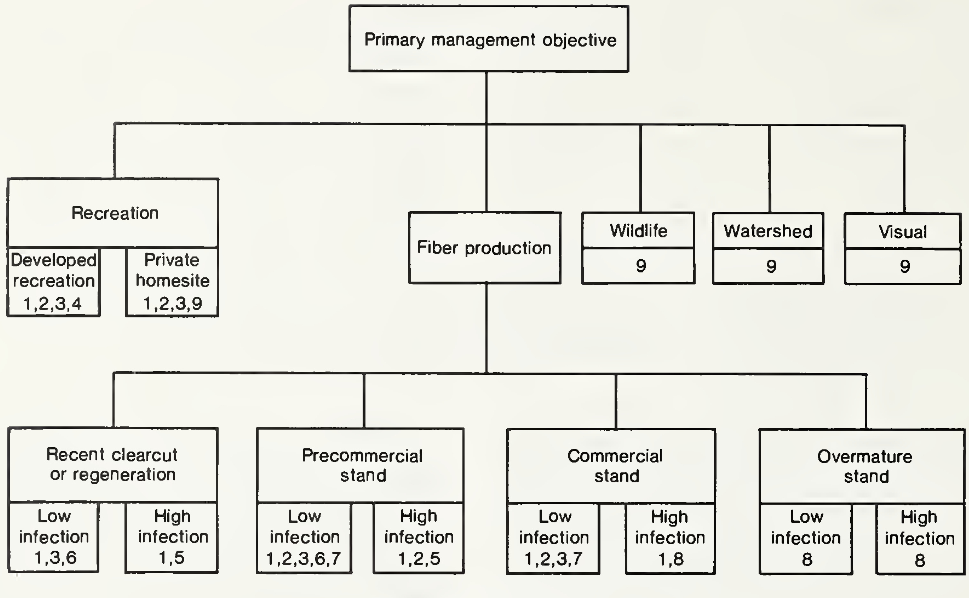
- Dwarf mistletoes are obligate parasites; that is, they require a living host to survive. Once an infected tree or branch is cut, the mistletoe dies. There is no need to destroy the slash for disease control.
- They are generally host specific; that is, they are usually confined to a single host species or group of closely related species. Immune or lightly infected species can be favored during stand treatments (fig. 21).

Table 9.—Annual mortality and growth loss caused by *Arceuthobium americanum* in commercial lodgepole pine forests.[1]

State	Area infested (1,000 acres)	Annual loss (1,000 ft^3)
Northern Rocky Mountain Region		
Montana	1,601	16,964
Northern Idaho	104	1,244
Rocky Mountain Region		
Colorado[2]	518	4,603
Eastern Wyoming[2]	361	4,958
Intermountain Region		
Southern Idaho	919	11,438
Nevada	6	74
Utah	206	2,571
Western Wyoming	242	2,850
Pacific Northwest Region		
Oregon	900	6,462
Washington	360	3,648
Total	5,217	54,812

[1]*These losses were compiled from USDA Forest Service estimates and reports; the states are grouped by USDA Forest Service Region.*

[2]*National forest lands only.*



Management Options

1. Survey for dwarf mistletoe infection.
2. Run data through the RMYLD program to predict yields.
3. Favor of plant tree species that are immune or resistant to LPP dwarf mistletoe.
4. Prune witches' brooms and infected branches. Re-examine pruned trees within five years for new and overlooked infection.
5. Destroy the stand and regenerate.
6. Fell nonmerchantable infected trees.
7. Sanitation thin.
8. Harvest and regenerate the stand.
9. Do nothing.

Figure 21.—Lodgepole pine dwarf mistletoe management decision key.

– Their life cycles are relatively long compared to other tree disease organisms. The development of mature mistletoe plants from seeds takes 2 to 8 years. From a practical standpoint, these long life cycles mean that the amount of infection increases relatively slowly. If a stand is properly treated, dwarf mistletoe should not be a serious problem in subsequent rotations.

– Dwarf mistletoes spread slowly through stands. Seed dispersal is usually limited to within 60 feet (20 m) from a tall, isolated tree. In even-aged stands, spread is even more limited and averages 1 to 2 feet (0.3–0.6 m) per year. Long distance dispersal of seeds by birds and mammals occurs (Nicholls et al. 1984), but so infrequently that it has little significance to management programs.

– Infected trees and stands are easy to detect because of the presence of dwarf mistletoe plants, branch and stem swellings, and witches' brooms. Heavily infested stands show decline and mortality. However, a complicating factor in some lodgepole pine stands is the frequent occurrence of non-mistletoe brooms termed "stimulation brooms" (Hawksworth 1961) (table 10, Plate III). The stimulation brooms are most common in residual trees left in cut-over areas. Detailed surveys are an essential ingredient of successful control programs (appendix II). Several survey methods have been developed to determine the distribution and intensity of infection (Dooling 1978). The 6-class dwarf mistletoe rating (DMR) system is an easily learned and applied numerical rating system that is widely used throughout the western coniferous forests to assess dwarf mistletoe infection levels in individual trees and stands (Hawksworth 1977) (fig. 22).

Successful strategies have been developed specifically for dwarf mistletoe control (Plate VI). However, these practices need to be integrated into plans that also seek to reduce susceptibility of stands to mountain pine beetle, *Dendroctonus ponderosae*. Both pests need to be consid-

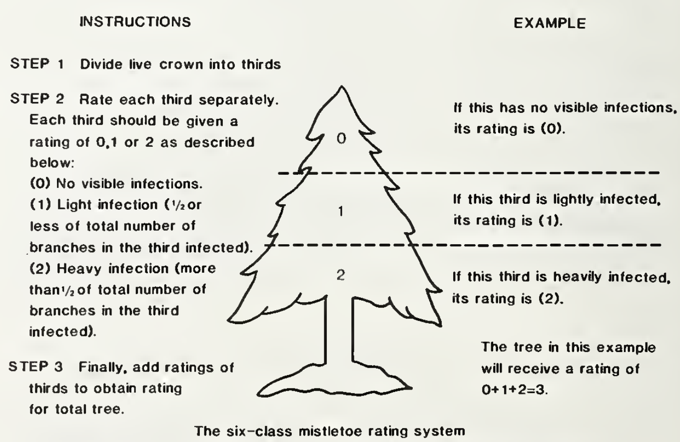


Figure 22.—The 6-class dwarf mistletoe rating system.

Table 10.—Comparison of dwarf mistletoe and stimulation brooms in lodgepole pine (Hawksworth 1961).

Characteristic	Dwarf mistletoe brooms	Stimulation brooms
Presence of dwarf mistletoe shoots or basal cups	Yes	No
Number and orientation of branches in broom	Many branches. Tips point upward.	Relatively few branches. Tips may point upward or sideways.
Crown class of tree	Any	Mainly suppressed or intermediates. Broken-off or spike-topped trees of any crown class.
Abundance	Usually several trees with brooms occur together. May be several brooms per tree.	Broomed trees are usually scattered. Usually few brooms per tree.
Location of brooms	May occur at any height or at any distance from the bole.	Usually below 30 feet and at or near bole.
Occurrence of dead brooms	Usually found on other trees in the immediate vicinity and sometimes on trees with living brooms.	None

ered in multiple resource management, because infestations affect even flow and sustained yield of the timber resource, complicate the conversion of unmanaged to managed forests, disrupt management plans, and affect local, regional, and national economics (McGregor and Cole 1985). In addition, infestations affect recreation and aesthetics, increase fire hazards, and affect watershed management. Mountain pine beetle may increase the proportion of trees infected by dwarf mistletoe through selective attack and resulting tree mortality in the stand, thus increasing the potential spread of dwarf mistletoe in the remaining stand.

In both cases, the objectives of pest management are to reduce pest incidence and intensity and to create a more healthy, pest-resistant forest.

Strategies are designed either to prevent or suppress the disease, depending upon the age of the stand and other management objectives. Because it is much more effective to prevent the establishment of mistletoes than to remove them from infested stands or replace severely infested stands, the priorities in control programs should be placed on prevention.

- Design treatment units to take advantage of natural or manmade barriers (such as roads, streams, non-susceptible forests, openings, or meadows) that prevent reinvasion from adjacent infested stands.
- Remove all infected trees before an area is planted or naturally regenerated.
- Use clearcuts to advantage when harvesting infested stands. Long, narrow cut strips should be avoided.
- Regenerate stands with the shelterwood method using mistletoe-free or lightly infected residual trees. If infected trees must be left (for instance, in areas sensitive to visual quality objectives), they should be removed before regeneration is 3 feet (1 m) tall or 10 years old.
- Select non-susceptible tree species when regenerating a stand or making intermediate entries.

These strategies all reduce the likelihood of dwarf mistletoe spreading into subsequent stands. When a stand is already infested, all infected overstory and then infected understory trees can be removed. This technique, known as sanitation-thinning, can be applied in lightly infested stands. Crop trees should be disease free. However, lightly infected trees may be retained, if necessary, to meet minimum stocking guides. Replacing severely infested stands with healthy stands by clearcutting, roller chopping, or prescribed burning and regenerating may be recommended for heavily infested stands.

The techniques to be used depend on individual stand conditions including stand age and structure, stand density, species composition, number of years to harvest, mistletoe incidence and distribution, and length of time the stand has been infested. Valuable tools—tree and stand growth models and dwarf mistletoe infection models—are available to help the resource manager simulate yields of infected trees and stands (Edminster 1978). Yields for a stand can be predicted under various management regimes and compared to no treatment. By comparing outputs and economic analyses of control costs, the manager can choose the best treatment alternative for each infested stand.

The effects of dwarf mistletoes on a stand depend on a combination of the intensity of infection, stand density, and stand structure. For a given intensity of infection, effects are most pronounced in dense stands. Table 11 shows the estimated percent volume loss to mistletoe

Table 11.—Estimated percent volume loss to dwarf mistletoe in relation to infection intensity and growing stock level. [(Site index 60, thinning interval 20 years) (Van der Kamp and Hawksworth 1985)].[1]

Percent volume loss	Infection intensity (DMR) at growing stock level (ft^2/acre)		
	60	100	140
10	2.1	1.5	1.3
20	2.7	2.0	1.6
30	3.2	2.5	2.0
40	3.7	3.1	2.5
50	4.3	3.6	3.0

[1]*For example, if the forest manager wants to keep mistletoe-caused losses to 10% using a growing stock level of 60, he needs to reduce the residual stand DMR to 2.1.*

in relation to infection intensity and growing stock level. For example, for stands rated as DMR 2 at age 60, estimated volume reduction is about 10%, 20%, and 30% for stands of GSL 60, 100, and 140 ft^2/acre (13.8, 23.0, and 32.1 m^2/ha), respectively. Another way to use this table is to decide what level of loss is acceptable, and then adopt management treatments to keep the infection below the given stand rating. For example, if a 30% loss can be tolerated, stand mistletoe ratings should be kept below DMR 3.2 for GSL 60 ft^2/acre (13.8 m^2/ha), DMR 2.5 for 100 ft^2 (23.0 m^2), and DMR 2.0 for 140 ft^2 (32.1 m^2).

Recently Harvested and Regenerated Stands

The opportunity to control dwarf mistletoe is greatest at the time of final harvest and, secondly, in recently regenerated stands, 5 to 15 years old. Sanitation is the primary emphasis of management in stands of this age.

The greatest dwarf mistletoe threat to regeneration exists where harvest of the previously infested stand was incomplete, and infected residual trees were left standing on the site. These residuals may have been left because they were of no merchantable value. Timber contracts now stipulate felling of diseased, nonmerchantable trees to prevent infection of the regeneration; but, unfortunately, dwarf mistletoe control was not adequately addressed in many past timber sales. Therefore, remedial work is needed in such stands.

Infected residuals over 6 feet (2 m) in height should be felled. Shorter infected trees pose little threat, because infections will be located in the lower half of the crown and dwarf mistletoe seed dispersal will be minimized. Also, bole infections on these trees usually will kill very small trees. All visibly infected trees, however, should be removed during subsequent precommercial stand entries.

Infected trees along the edges of openings should be felled to prevent infection of the regeneration. As a general rule, infected edges should be cut back 60 feet (18 m) before the regeneration is 3 feet (1 m) tall or 10 years old.

If infected residuals have been present for more than about 10 years, the regeneration is probably also infected and will require subsequent sanitation to prevent serious losses in the future. A survey of the regeneration to determine the amount of infection will indicate if sufficient stocking of noninfected and acceptable trees is available for future crop trees. If the infested residual stand has been present for 20 or more years and the regeneration is heavily infected, then it may be necessary to artificially regenerate the site. Guidelines are available based on stand age and average stand DMR (Hawksworth et al. 1977).

Precommercial Stands

The appropriate control measure in stands of this size class should be based on survey data that include the size and location of dwarf mistletoe-infested areas within the stand, the approximate number and location of infected residual trees, and the number of potential crop trees. In most precommercial stands, an intensive, systematic survey provides the best method for collecting these data. Data points (fixed or variable radius plots) should be arranged in a grid pattern over the entire area to insure adequate coverage (appendix II). Spacing between plots should not exceed 10 chains (200 m); 5-chain intervals (100 m) or less are recommended in infested stands. The location of dwarf mistletoe infestations observed when traversing from plot to plot also should be noted.

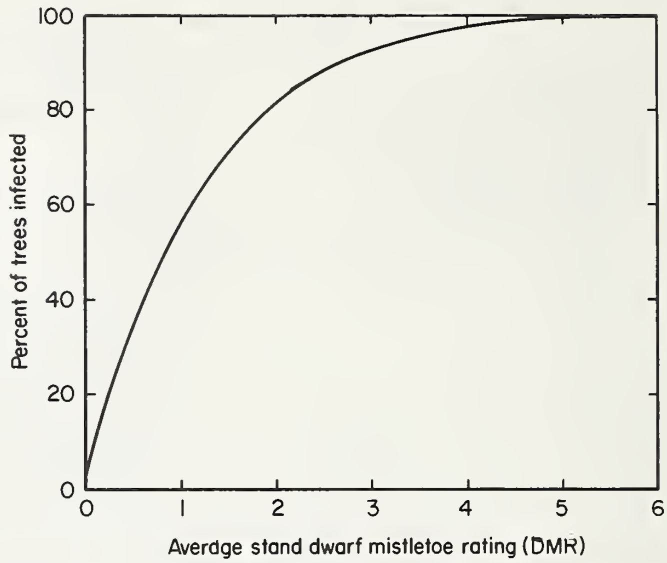


Figure 23.—Relationship between percent of trees infested an average stand dwarf mistletoe rating (DMR) for unmanaged lodgepole pine stands.

Sanitation should be an integral part of all stand entries for thinning, especially in lightly infested precommercial stands from which all overstory or residual infected stems have been felled or killed. The degree of infestation in the stand, not strictly stand age, is the best criterion to decide whether sanitation is practical. A general guide is that stands with more than 40% of the trees infected (average stand rating greater than DMR 0.5) (fig. 23) are too heavily infested to attempt strict sanitation cutting or the removal of all infected trees. In such stands, removal of so many trees will reduce stocking below minimal acceptable levels (Hawksworth 1978, Hawksworth et al. 1977).

The highest priority for precommercial sanitation thinning is stands 10 to 20 years old with less than 40% infection. Potential crop trees should have no visible mistletoe infections. Stands should be thinned and sanitized only if evaluations indicate that minimum acceptable stocking can be achieved with noninfected trees. Severely infested stands that lack acceptable stocking of potential crop trees should be harvested or destroyed (if no products can be salvaged) and the site regenerated. The RMYLD program (Edminster 1978, Hawksworth 1978) can be used to project the growth of the stand to determine whether or not replacement is the best alternative. In stands where potential crop trees average 2 inches

d.b.h. or larger, the order of priority for crop tree selection is:

1. Non-infected dominants and co-dominants.
2. Dominants and co-dominants with mistletoe confined to branches in the lower one-third of live crown (DMR less than 2.0).
3. Intermediates with no visible infection.
4. Dominants and co-dominants with mistletoe confined to less than one-half of the branches in the lower two-thirds of the live crown (DMR less than 3.0). Non-infected intermediates should be selected over DMR class 2 or 3 trees.

If acceptable stocking cannot be obtained within these guidelines, then perhaps the stand should not be thinned. Thinning crews must be able to recognize infections if sanitation treatments are to be effective. Precommercially sanitized stands should not be treated again for mistletoe control until they can be treated during a commercial timber sale.

Suggested guidelines for stocking of sapling and merchantable-sized stands are presented in table 12.

Commercial Stands

Survey information that includes the location and intensity (average stand DMR) of dwarf mistletoe infection is essential to determine the need for control. Yield projections of these stands are invaluable to determine whether infection levels are high enough to influence growth and yield. Sanitation-thinning is recommended only where the stand DMR is 3.0 or less and removal of infected trees does not reduce stocking levels below the accepted minimum. Severely infested stands that lack acceptable stocking of potential crop trees should be harvested early and the site regenerated. If a mixture of non-susceptible species is present, then those species should be favored for regeneration of the stand.

Infested, mature stands that are scheduled for harvest and regeneration offer the greatest opportunity to control the disease by replacement of the stand with mistletoe-free regeneration. Heavily infested stands with sufficient tree seed sources may be clearcut and the cone-bearing tops scattered to obtain natural regeneration, or the slash may be burned and the site planted. Clearcuts in infested stands should have as large an area/perimeter ratio as allowable to minimize reinvasion from infected trees along bordering stands. Narrow strips should be avoided. Cutting units should be no less than 20 acres (8 ha) to minimize the edge effect (fig. 24). However, where natural regeneration is desired in areas with non-serotinous cones, smaller cutting units may be needed (Alexander 1986) as border trees provide the only seed source. Wherever possible, cutting boundaries should be located in non-infested stands, non-susceptible timber types, and natural or manmade openings to prevent reinfection of the regenerated stand from adjacent stands.

In areas where retention of infected trees is needed to protect regeneration from adverse climate conditions or where the visual resource is critical to protect, a shelterwood prescription (partial retention of the stand) may be required. However, once the site has regenerated and is established (within 5 to 10 years), all infected trees should be felled or harvested to prevent infection of the regeneration.

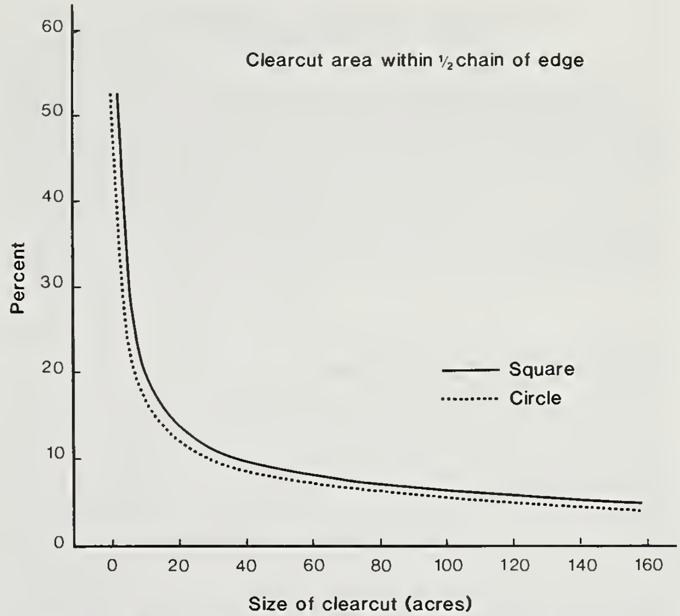


Figure 24.—Relationship between clearcut area and proportion of the clearcut within 1/2 chain (10 m) of the edge, the effective maximum distance of dwarf mistletoe spread.

Table 12.—Adequate, marginal, and inadequate stocking for disease-free sapling and merchantable-sized stands of lodgepole pine.

Lodgepole pine	Degree of stocking: Adequate	Marginal	Inadequate
Sapling stands (number of disease-free stems per acre)	>250	150–250	<150
Merchantable-size stands (basal area ft^2 of disease-free stems per acre)	>70	40–60	<40

Management of Stands for Other Than Fiber Production

Although the debilitating effects of mistletoe on tree growth and fiber production are well documented, their effects on other resource values have not been fully assessed. The effects on recreation, wildlife, watershed, and visual quality may be positive or negative depending upon the resource manager's objectives for the area in question.

Developed Recreation Sites

There are several different classes of recreation use, including multiple-use areas where recreation is a secondary use and others where it is the primary use (Smith 1978). Others include wilderness areas where management activities are minimized, dispersed recreation areas, and the developed recreation areas, such as campgrounds, picnic areas, ski areas, visitor centers, and other administrative sites. This discussion focuses on the intensively used, developed recreation site where dwarf mistletoe control may be needed to protect various recreation values (Plate VII).

The primary objective of dwarf mistletoe control in these sites is to reduce the negative effects of the disease on tree vigor and longevity and to prevent disease spread into non-infested areas. Effects of dwarf mistletoes on tree growth rates are of less concern, except as growth loss eventually affects tree vigor and mortality. Silvicultural techniques discussed earlier for commercial forests (clearcutting, sanitation thinning) are less acceptable alternatives in developed sites; thus, emphasis is placed on the introduction of non-susceptible species in the understory or on favoring existing non-susceptible species. Pruning mistletoe infected branches, broomed branches, and establishing buffers to prevent spread of the disease can also be used.

Pruning infected branches usually is not practical in commercial stands because of the high cost and difficulty of removing infections; also, repeated treatments are needed to eliminate latent infections. Pruning may be practical, however, to save trees that are needed for stocking and to prolong the life of high value trees in developed recreation, administrative, or home sites (Brown 1978, Hawksworth et al. 1968, Lightle and Hawksworth 1973). Candidate trees for pruning should only be infected in the lower half of the crown, have a DMR of 3 or less, and have no bole infections (where the bole is less than 5 inches in diameter). Infections on parts of the bole over 5 inches have little impact on growth and produce few seeds; therefore, they are of little management concern (Walters 1974). For branch infections on parts of the main stem under 5 inches in diameter, dwarf mistletoe shoots should be at least 4 inches from the bole (Hawksworth and Johnson 1961). Otherwise, the mistletoe's root system will have already entered the trunk and will produce a bole infection.

All live branches in the two whorls above the highest visibly infected branch should be pruned, but try not to remove more than one-half of the tree's live crown. Pruning cannot eliminate all infections because many may be latent, so pruned trees should be re-examined and new or overlooked infections removed in 3–5 years.

Broom pruning may also be effective in prolonging the life of individual trees (Lightle and Hawksworth 1973). The emphasis is on removing branches with witches' brooms rather than removing all visibly infected branches. Studies have shown dramatic recovery in crown vigor in broom-pruned lodgepole pines (Plate VII).

Some research on chemicals that could be applied to infected trees to reduce or kill mistletoe shoots has been reported. Recently, the plant growth regulator ethephon (an ethylene-releasing agent) has been shown to cause premature shoot abscission of *A. pusillum* on spruce in the Lake States and *A. americanum* on lodgepole pine in Colorado (Livingston et al. 1985, Nicolls et al. 1987). This material could be sprayed on infected trees before mistletoe seed dispersal to prevent new infections on existing understory regeneration or planted susceptible tree species. Applications at 3- to 6-year intervals may be necessary because only the aerial portions of the shoots are affected, and resprouting will occur from the endophytic system. This product appears to have promise for reducing dwarf mistletoe spread in recreational forests, but it needs more testing before it can be recommended for operational use.

In planning the location of new recreation sites, dwarf mistletoe infested stands should be avoided, or at least treated, before planning designs are initiated.

Dwarf mistletoe infected trees are more susceptible to attack by secondary bark beetles (*Ips* sp.). Large brooms, dead tops, and witches' brooms are a hazard to recreationists. Opening infested stands only serves to intensify the rate of new infections, resulting in more rapid tree decline and mortality.

Wildlife

Lodgepole pine forests generally are low in variety of plant species and understory vegetation (Basile 1975). The production of forage and nutritional value is limited for game and livestock use (Urness 1985). Alexander (1986) discussed the implications of silvicultural treatments in lodgepole pine on wildlife. Dwarf mistletoe may cause openings in the canopy of infected stands as trees decline in vigor and die, thus creating more favorable conditions for understory plant growth. As these openings regenerate to either the same tree species or other tree species and understory plants, greater vegetation diversity will result. Profound changes in both stand structure and species composition may occur (Tinnin 1984). The mistletoe plants themselves provide a food source for some rodents, birds, and insects (Hawksworth 1975). Mistletoe-killed trees provide nesting sites for snag-dependent bird species. Witches' brooms also provide cover and nesting sites for many birds and mammals (Nicholls et al. 1984).

An example of the potential conflicts between recommendations from dwarf mistletoe control and wildlife

compared with timber production appears in the forest management plan for the Bridger-Teton National Forest in Wyoming (B. Tkacz, personal communication, 1986). The management emphasis is on wildlife, especially elk, and the plan calls for small clearcuts (10 acres or less) in lodgepole pine and leaving reproduction adjacent to residual stands until the young trees are at least 10 feet high, to provide elk hiding cover. Thus, if the residual stands are infected with mistletoe, the parasite will be well established in the young stand by the time the overstory is removed, so the manager must weigh the alternatives of wildlife habitat enhancement against future losses in timber production.

Watershed

Swanson (1985) and Alexander (1986) reviewed manipulation of lodgepole pine forests to augment water yields. However, data on mistletoe effects are lacking. Dwarf mistletoe may indirectly alter streamflow by localizing snow accumulations in open areas created in diseased stands. Hoover and Leaf (1966) noted that more snow tends to accumulate on witches' brooms than on healthy lodgepole pine branches.

Visual Quality

The effects of dwarf mistletoes on aesthetics and visual quality generally would be considered negative through reduced tree vigor, increased mortality, and increased fuel accumulations and susceptibility to fire. Research on pines infected by limb rust has quantified visual quality of diseased trees (Baker and Rabin 1988), but such studies have not yet been made for mistletoe-infected trees. Isolated broomed trees may appear to some recreationists as lending "character" to the landscape and being more photogenic; however, expanses of infected stands are unappealing.

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APPENDIX I. EXAMPLES OF RMYLD YIELD PROJECTIONS FOR SELECTED STANDS

Examples of projected yields in dwarf mistletoe infested lodgepole pine stands using the RMYLD simulation program: Routt National Forest, northern Colorado are given in tables A–D.

A and B show projected yields over 80 years for a stand now 30 years old (site index, 60 feet; trees per acre, 2,700; average d.b.h., 2.0; 30% of trees infected; and stand dwarf mistletoe rating, 0.4). A shows projected yields if the stand has no treatment (2,100 merchantable cubic feet per acre and no board foot volume). B shows the projected yield if the stand is thinned to growing stock level 100 at 20 year intervals (4,410 merchantable cubic feet and 17,800 board feet per acre).

C and D show projected yields over 40 years for a stand now 70 years old (site index, 60 feet; trees per acre, 1,500; average d.b.h., 5.0; 80% of trees infected; and stand dwarf mistletoe rating, 2.1). C shows projected yield if the stand has no treatment (2,810 merchantable cubic feet per acre and no board foot volume). D shows the projected yields if the stand is thinned to growing stock level 100 at age 70 and 90 (3,490 merchantable cubic feet and 11,400 board feet per acre).

APPENDIX II. SURVEY METHODS FOR LODGEPOLE PINE DWARF MISTLETOE

Extensive Surveys

The objective of extensive surveys is to determine the general distribution of dwarf mistletoe over large areas for assessment of losses and long-term planning on a forest-wide and regional basis. The sampling design may be random or systematic. Sampling intensity is usually less than 1% of the area.

Graham (1964) determined the distribution of several mistletoes, including *A. americanum*, in lodgepole pine by sampling townships at 10 locations. The starting point of each sample line was predetermined from a point on the road nearest the center of each township and plots were spread along each line at 10-chain intervals. Sample plots consisted of three concentric circular areas: 1/5 acre for sawtimber, 1/50 acre for pole size trees, and 1/500 acre for saplings.

Various types of roadside surveys have been used for lodgepole pine dwarf mistletoe (Hawksworth 1958a, Hoffman and Hobbs 1985, Johnson et al. 1981). Essentially they consist of driving all passable roads through the selected forest type, recording stand type, size class, and intensity of dwarf mistletoe infestation along a strip adjacent to the road. In addition, plots may be located at intervals within the sampled strip to gather more detailed data on tree diameter, height, age, and dwarf mistletoe rating. This type of survey works well to obtain forest-wide and regional information on the general distribution of the disease and loss at reasonable cost. Infrared aerial photography has been used successfully to detect mortality in black spruce caused by *A. pusillum* (Meyer and French 1967). Direct aerial detection is applicable for *A. americanum* in jack pine (Muir and Robins 1973) but not for lodgepole pine, because brooms are less dense and harder to discern from the air in the latter species.

Intensive Surveys

The objective of intensive surveys is to gather information on the distribution and location of infested stands or parts of stands for management planning and development of suppression programs. The level of sampling intensity usually is at least 10% of the area.

Stand or compartment examinations are the simplest and least expensive to conduct. The number of sample points is limited (about one plot per 10 acres) and may provide the accuracy and precision needed for good suppression planning. A combination of variable and fixed radius plots is used for tree data.

Walters and Brown (1973) and D. H. Brown (1975) compared three sampling techniques for determining presence and infection intensity of *A. americanum* in lodgepole pine: the Stage II compartment examination used in the Rocky Mountain Region (about one plot per 10 acres), a 1% fixed plot sample, and third nearest tree sample on two- and four-chain grids. An analysis of their data compared to a 100% survey indicated the third nearest tree sample on a four-chain grid gave acceptable precision at reasonable cost. However, because of the complex data analyses needed for the third-nearest tree method, fixed-area plots are recommended.

In high value recreation sites, a very detailed, intensive survey may be desired. Strip and plot samples may be used to cover most of the area.

APPENDIX I. PRINTOUT A - YIELDS PER ACRE OF LODGEPOLE PINE WITH NO THINNING, ROUTT NATIONAL FOREST, COLORADO.

SITE INDEX 60 FT. NO THINNING
VALUES IN TABLE ADJUSTED FOR 1.000 STOCKABLE AREA AND .000 DEFECT.

CHARACTERISTICS BEFORE AND AFTER THINNING											PERIODIC INTERMEDIATE CUTS						
STAND AGE YEARS	DMR	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	AVERAGE HEIGHT FT.	TOTAL VOLUME CU.FT.	MAI	MERCH. VOLUME CU.FT.	MAI	SAWTIMBER VOLUME BD.FT.	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	TOTAL VOLUME CU.FT.	MERCH. VOLUME CU.FT.	SAWTIMBER VOLUME BD.FT.	MERCH. CU.FT. SUBSAWLOG
30	.4	2700	59	2.0	24	600	20	0	0	0							
30	.4	2700	59	2.0	24	600		0		0	0	0	.0	0	0	0	0
40	.6	2434	112	2.9	30	1520	38	0	0	0							
50	.9	2177	145	3.5	34	2320	46	0	0	0							
50	.9	2177	145	3.5	34	2320		0		0	0	0	.0	0	0	0	0
60	1.2	1928	160	3.9	38	2900	48	0	0	0							
70	1.9	1688	170	4.3	42	3450	49	0	0	0							
70	1.9	1688	170	4.3	42	3450		0		0	0	0	.0	0	0	0	0
80	2.6	1439	173	4.7	46	3880	49	0	0	0							
90	3.3	1194	169	5.1	50	4150	46	860	10	0							
90	3.3	1194	169	5.1	50	4150		860		0	0	0	.0	0	0	0	0
100	4.0	963	159	5.5	54	4220	42	1410	14	0							
110	4.7	881	167	5.9	55	4570	42	2110	19	0							
											TOTAL YIELDS			4570	2110	0	2110

MERCH. CU. FT. - TREES 6.0 INCHES D.B.H. AND LARGER TO 4.0-INCH TOP.
BD. FT. - TREES 6.5 INCHES D.B.H. AND LARGER TO 6.0-INCH TOP.
AT AGE 30, 30 PERCENT OF THE TREES WERE INFECTED WITH DWARF MISTLETOE.
CULMINATION OF M.A.I. MERCH. CU. FT.--AGE= 110 MAI= 19.
CULMINATION OF M.A.I. TOTAL CU. FT.--AGE= 70 MAI= 49.

APPENDIX I. PRINTOUT B - YEILDS PER ACRE OF LODGEPOLE PINE, ROUTT NATIONAL FOREST, WITH THINNING IN SAME STAND AS A.

SITE INDEX 60 FT. 20-YEAR THINNING INTERVAL
THINNING INTENSITY-- INITIAL-100 SUBSEQUENT- 100
VALUES IN TABLE ADJUSTED FOR 1.000 STOCKABLE AREA AND .000 DEFECT.

CHARACTERISTICS BEFORE AND AFTER THINNING											PERIODIC INTERMEDIATE CUTS						
STAND AGE YEARS	DMR	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	AVERAGE HEIGHT FT.	TOTAL VOLUME CU.FT.	MAI	MERCH. VOLUME CU.FT.	MAI	SAWTIMBER VOLUME BD.FT.	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	TOTAL VOLUME CU.FT.	MERCH. VOLUME CU.FT.	SAWTIMBER VOLUME BD.FT.	MERCH. CU.FT. SUBSAWLOG
30	.4	2700	59	2.0	24	600	20	0	0	0							
30	.0+	900	11	1.5	22	110		0		0	1800	48	2.2	490	0	0	0
40	.2	B68	52	3.3	28	710	30	0	0	0							
50	.2	853	86	4.3	32	1340	37	0	0	0							
50	.0+	438	57	4.9	33	940		0		0	415	29	3.6	400	0	0	0
60	.1	434	82	5.9	39	1610	42	740	12	0							
70	.2	433	106	6.7	44	2350	46	1700	24	0							
70	.0+	298	84	7.2	45	1900		1500		0	135	22	5.5	450	200	0	200
80	.1	297	104	8.0	49	2560	49	2230	30	9200							
90	.1	297	123	8.7	53	3260	51	2960	35	12100							
90	.0+	211	97	9.2	53	2620		2410		9900	86	26	7.4	640	550	2200	0
100	.1	209	114	10.0	56	3240	52	3040	38	12800							
110	.1	209	131	10.7	59	3890	53	3660	40	15600							
											TOTAL YIELDS			5870	4410	17800	200

MERCH. CU. FT. - TREES 6.0 INCHES D.B.H. AND LARGER TO 4.0-INCH TOP.
BD. FT. - TREES 6.5 INCHES D.B.H. AND LARGER TO 6.0-INCH TOP.
INITIAL THINNING FROM ABOVE ALLOWED IN STANDS WITH DWARF MISTLETOE.
D.M.R. ABOVE WHICH PERIODIC THINNINGS WILL NOT BE EXECUTED - 3.0.
AT AGE 30, 30 PERCENT OF THE TREES WERE INFECTED WITH DWARF MISTLETOE.
NO NONCOMMERCIAL THINNINGS ALLOWED.
CULMINATION OF M.A.I. MERCH. CU. FT.--AGE= 110 MAI= 40.
CULMINATION OF M.A.I. TOTAL CU. FT.--AGE= 110 MAI= 53.

APPENDIX I. PRINTOUT C - YIELDS PER ACRE OF LODGEPOLE PINE WITH NO THINNING, ROUTT NATIONAL FOREST, COLORADO

SITE INDEX 60 FT. NO THINNING
VALUES IN TABLE ADJUSTED FOR 1.000 STOCKABLE AREA AND .000 DEFECT.

		CHARACTERISTICS BEFORE AND AFTER THINNING									PERIODIC INTERMEDIATE CUTS						
STAND AGE YEARS	DMR	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	AVERAGE HEIGHT FT.	TOTAL VOLUME CU.FT.	MAI	MERCH. VOLUME CU.FT.	MAI	SAWTIMBER VOLUME BD.FT.	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	TOTAL VOLUME CU.FT.	MERCH. VOLUME CU.FT.	SAWTIMBER VOLUME BD.FT.	MERCH. CU.FT. SUBSAWLOG
70	2.1	1500	205	5.0	43	4210	60	740	11	0							
70	2.1	1500	205	5.0	43	4210		740		0	0	0	.0	0	0	0	0
80	2.8	1223	187	5.3	46	4260	53	1150	14	0							
90	3.5	1007	172	5.6	50	4270	47	1570	17	0							
90	3.5	1007	172	5.6	50	4270		1570		0	0	0	.0	0	0	0	0
100	4.2	806	158	6.0	54	4240	42	2100	21	0							
110	4.9	732	164	6.4	55	4500	41	2810	26	0							
											TOTAL YIELDS			4500	2810	0	2810

MERCH. CU. FT. - TREES 6.0 INCHES D.B.H. AND LARGER TO 4.0-INCH TOP.
BD. FT. - TREES 6.5 INCHES D.B.H. AND LARGER TO 6.0-INCH TOP.
AT AGE 70, 80 PERCENT OF THE TREES WERE INFECTED WITH DWARF MISTLETOE.
CULMINATION OF M.A.I. MERCH. CU. FT.--AGE= 110 MAI= 26.
CULMINATION OF M.A.I. TOTAL CU. FT.--AGE= 70 MAI= 60.

APPENDIX I. PRINTOUT D. YIELDS PER ACRE OF LODGEPOLE PINE, ROUTT NATIONAL FOREST, WITH THINNING IN SAME STAND AS C.

SITE INDEX 60 FT. 20-YEAR THINNING INTERVAL
THINNING INTENSITY-- INITIAL-100 SUBSEQUENT- 100
VALUES IN TABLE ADJUSTED FOR 1.000 STOCKABLE AREA AND .000 DEFECT.

		CHARACTERISTICS BEFORE AND AFTER THINNING									PERIODIC INTERMEDIATE CUTS						
STAND AGE YEARS	DMR	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	AVERAGE HEIGHT FT.	TOTAL VOLUME CU.FT.	MAI	MERCH. VOLUME CU.FT.	MAI	SAWTIMBER VOLUME BD.FT.	TREES NO.	BASAL AREA SQ.FT.	AVERAGE D.B.H. IN.	TOTAL VOLUME CU.FT.	MERCH. VOLUME CU.FT.	SAWTIMBER VOLUME BD.FT.	MERCH. CU.FT. SUBSAWLOG
70	2.1	1500	205	5.0	43	4210	60	740	11	0							
70	.3	364	32	4.0	40	630		0		0	1136	173	5.3	3580	740	0	740
80	.5	358	55	5.3	44	1210	60	330	13	0							
90	.8	355	77	6.3	48	1840	60	1130	21	0							
90	.5	338	76	6.4	48	1810		1130		0	17	1	3.3	30	0	0	0
100	.8	337	98	7.3	51	2500	61	2010	28	0							
110	1.1	337	118	8.0	54	3170	62	2750	32	11400							
											TOTAL YIELDS			6780	3490	11400	740

MERCH. CU. FT. - TREES 6.0 INCHES D.B.H. AND LARGER TO 4.0-INCH TOP.
BD. FT. - TREES 6.5 INCHES D.B.H. AND LARGER TO 6.0-INCH TOP.
INITIAL THINNING FROM ABOVE ALLOWED IN STANDS WITH DWARF MISTLETOE.
D.M.R. ABOVE WHICH PERIODIC THINNINGS WILL NOT BE EXECUTED - 3.0.
AT AGE 70, 80 PERCENT OF THE TREES WERE INFECTED WITH DWARF MISTLETOE.
NO NONCOMMERCIAL THINNINGS ALLOWED.
CULMINATION OF M.A.I. MERCH. CU. FT.--AGE= 110 MAI= 32.
CULMINATION OF M.A.I. TOTAL CU. FT.--AGE= 110 MAI= 62.

Hawksworth, Frank G.; Johnson, David W. 1989. Biology and management of dwarf mistletoe in lodgepole pine in the Rocky Mountains. Gen. Tech. Rep. RM-169. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.

This publication synthesizes the vast literature on lodgepole pine dwarf mistletoe (*Arceuthobium americanum*) and adds some new information on biology of the parasite. Although dwarf mistletoe has been recognized as a serious parasite of lodgepole pine for more than 75 years, its routine operational control through forest management has been primarily a development over the past two decades. This report discusses silvicultural control of dwarf mistletoe in various types of stands where fiber production is the primary goal, and also in forests used mainly for recreation.

Keywords: *Arceuthobium*, *Pinus contorta*, damage, control, tree diseases, dwarf mistletoe, lodgepole pine.

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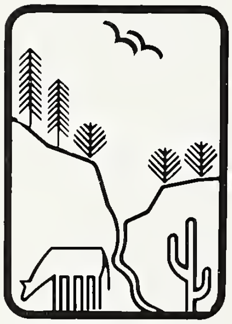
Rocky Mountain Forest and Range Experiment Station

Rocky Mountains



Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526